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Variation in Certain Wood Properties of Eastern White Pine

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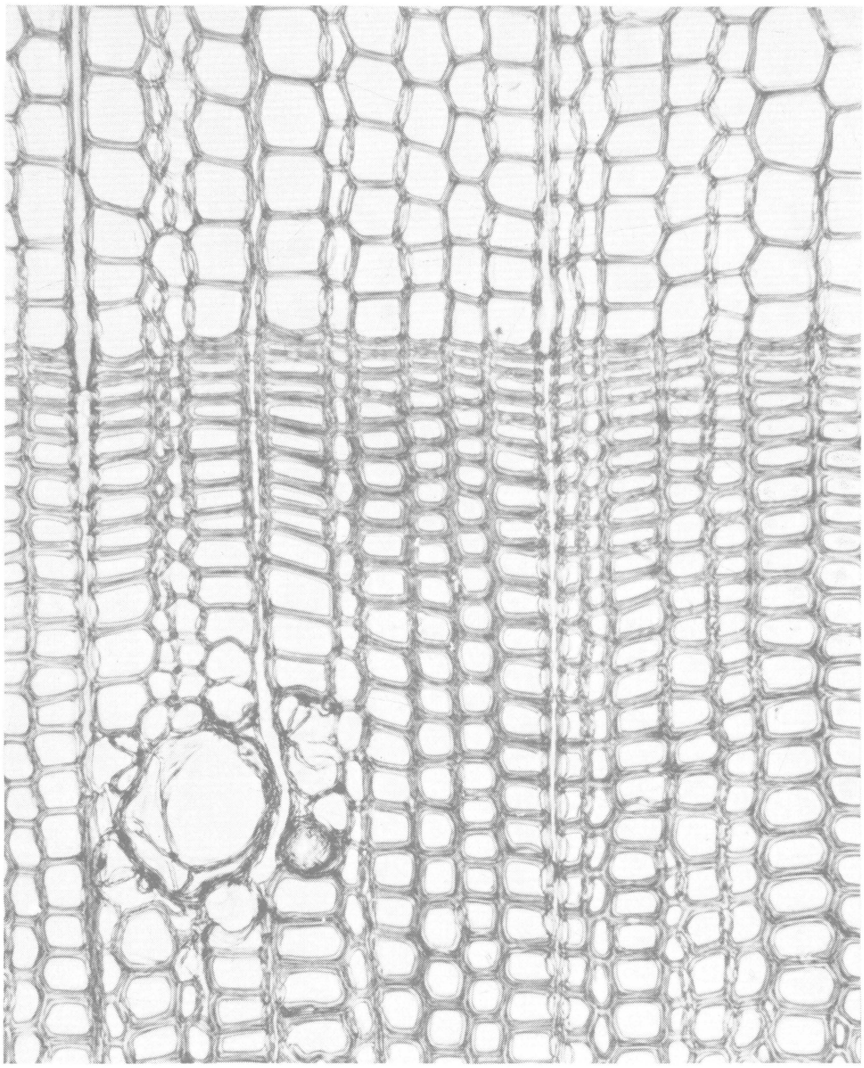

OHIO AGRICULTURAL RESEARCH AND DEVELOPMENT CENTER
Wooster, Ohio

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ON THE COVER: Transverse section of white pine.

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VARIATION IN CERTAIN WOOD PROPERTIES OF EASTERN WHITE PINE[1, 2]

A. N. FOULGER[3]

INTRODUCTION

The objectives of the study were: (1) to examine variation in cell number in the annual ring, ring width, percentage of latewood, longitudinal shrinkage, and specific gravity existing at different heights in the stem and at different distances from the pith in eastern white pine (*Pinus strobus* L.); and (2) to examine to what extent change in the above variables is associated with seasonal levels of soil moisture availability.

Wood properties vary not only with position in the stem but also due to position of the tree in its environment. The many factors comprising the site—weather, topography, and competing vegetation—all exert an influence on the tree to a greater or lesser degree.

In this study, the primary concern was the effect of position in the main stem on wood structure and properties, with an ancillary study of the extent to which soil moisture deficits modify the variation pattern due to position. It is not suggested that soil moisture deficit typifies the effect of the entire environment. However, soil moisture availability is one of the major influences on tree growth and, as determined in this study, is an estimate of soil type, precipitation, and air temperature effects in combination.

This intensive study of three codominant trees from a single site was designed primarily to establish a characteristic pattern of variation in several wood properties within the stem. After determining this pattern, it should be possible to design a system of less intensive sampling, using large increment cores, to compare the wood structure pattern of other eastern white pines growing under different conditions. It is fully realized that data from three trees on one site do not constitute a tenable base for the total evaluation of the intrinsic and extrinsic factors controlling wood formation in eastern white pine. However, they provide one of the bases from which to explore the structure of the white pine stem.

Investigation of wood property-growth condition relationships has proceeded rapidly during the past few years. The broad field of moisture-tree growth relationships has been thoroughly reviewed by Glock (14), Kramer and Kozlowski (20), and in conifers by Zahner (42). Research covering the entire range of environmental effects on wood properties has been summarized in a recent Tappi bibliography (35).

In general approach, this study was similar to those of Duff and Nolan (10), Richardson (28), and Smith and Wilsie (32).

Duff and Nolan, after describing three axes within the stem of red pine along which meaningful comparisons of anatomic properties might be made, showed the existence of a repetitive pattern of ring width along successive growth sheaths. This pattern illustrated a strong positional effect within the tree, with curves from a series of growth sheaths from apex to base having the same general form, particularly within the top internodes.

Using the same technique with Corsican pine, Richardson presented families of curves illustrative of a similar physiological position influence on tracheid length within the stem.

Combination of soil moisture deficits with growth sheath measurements in loblolly pine for specified growing seasons permitted Smith and Wilsie to develop ring width, percentage of latewood, and specific gravity relationships which demonstrated the effects of soil moisture deficit on the values within the growth sheath.

Specific gravity is of considerable economic importance. It describes the amount of actual wood substance in a sample and is frequently indicative of the wood's utility in terms of strength, machinability, pulping, etc. Therefore, stem analyses to determine variation of this property within the stem have been conducted on numerous occasions. However, these have been accompanied rather infrequently by concurrent examinations of other stem variables, although the work of Hamilton (15) with red oak is an exception. The literature on specific gravity has been thoroughly reviewed by Spurr and Hsiung (33), Larson (21), and more recently by Paul (26).

While specific gravity has been studied thoroughly, longitudinal shrinkage has received compara-

[1]Based on a dissertation presented in partial fulfillment of the requirements for the Ph. D. degree, University of Michigan.
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tively little attention. Longitudinal shrinkage, which is much less than shrinkage in either the radial or the tangential directions, generally is greatest close to the pith. It becomes important in boards with only one edge within 10 rings of the pith. In such instances, the difference in shrinkage between the inner and outer edges of the board may be sufficient to cause severe warping.

Koehler (19) and Pillow and Luxford (27) reported a direct relationship between ring width and longitudinal shrinkage, with the wider rings showing greater shrinkage.

Cockrell (5) was unable to agree with this conclusion, stating that when marked longitudinal shrinkage occurred in coniferous wood, it could be traced to proximity to the pith, compression wood, or irregular grain. Previously Cockrell (4) had proposed a mathematical explanation of longitudinal shrinkage which he ascribed to a combination of four factors: the interaction of chain molecules, fibril angle, cellulose chain-molecule length, and microcapillary width.

Recently Australian workers have shown interest in the longitudinal shrinkage of wood and in its variation within the stem, (7, 17).

LOCATION OF SAMPLE TREES

In March 1962, three codominant 52-year-old eastern white pines were selected from a stand planted in the fall of 1913. Trees 1 and 2 were within the stand and tree 3 was exposed slightly on the southeast. The trees were chosen on the basis of straightness of stem, absence of lean, and position in the canopy. Stem diagrams of the three trees are shown in Figure 1.

The particular white pine stand was chosen for its proximity to a weather station. It was less than ½ mile from the weather station at the Ohio Agricultural Research and Development Center, where weather data have been collected since 1887. Thus, daily temperature and precipitation readings were available for a location relatively close to the stand.

Meteorological studies have shown significant temperature and rainfall differences between stations inside and outside a forest boundary and experience indicates this to be true in the present study. Although the weather station observations do not give a definitive measure, it is assumed for this study that these data give a relative measure of conditions within the stand during its growth.

The average climate at Wooster is characterized by an evenly distributed rainfall without great temperature extremes. The average annual rainfall is 36 inches but has varied between 24 and 54 inches.

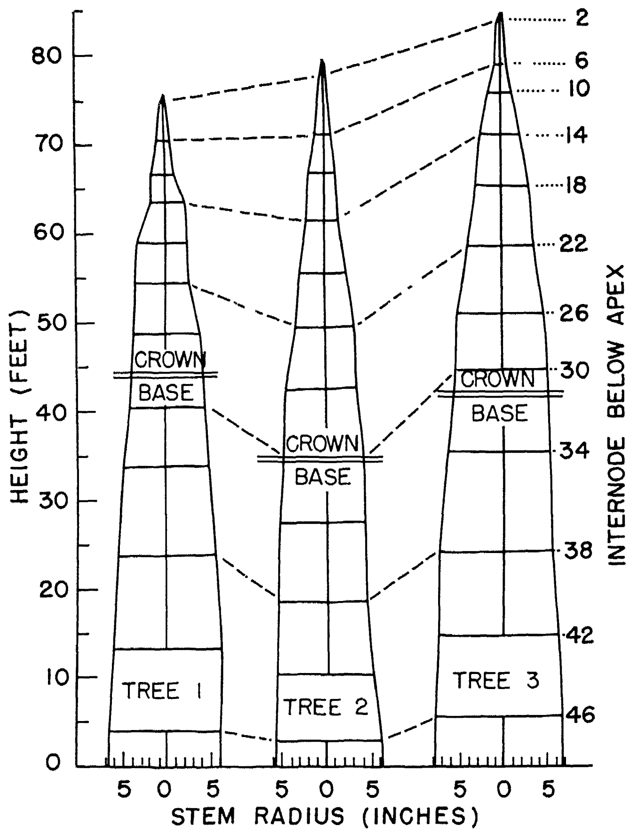


Fig. 1.—Stem diagram of sample trees.

Average precipitation figures for the four seasons are 7, 10, 11, and 8 inches for winter, spring, summer, and autumn respectively. Snowfall records give an average value of 35 inches per year, with 75 inches the recorded maximum.

Mean monthly temperatures, which range from 28.2° F. in January to 72.3° F. in July, and mean monthly rainfalls are listed in Table 1. A high temperature of 105° F. has been noted in August, while

TABLE 1.—Mean Monthly Rainfall and Mean Temperature at Wooster, Ohio, Based on Records for Years 1921 to 1950.

Month	Rainfall (inches)	Temperature (Degrees Fahrenheit)
January	2.84	28.2
February	2.20	29.3
March	3.23	37.7
April	3.07	48.1
May	3.82	58.6
June	4.13	68.4
July	3.68	72.3
August	3.40	70.4
September	2.98	64 4
October	2.17	52.9
November	2.52	40.7
December	2.42	30.5

the lowest, which occurred in January, was —24° F. The average growing season is 152 days, with the last killing frost recorded on May 10 and the first severe frost on October 7. On the average, precipitation occurs 129 days each year and there are 138 clear days.

COLLECTION OF SOIL DATA

A soil analysis was made to determine whether the sample trees had grown on a uniform soil type. Three pits were dug equidistantly around each tree, with the inner wall of the pit located 4 feet from the center of the tree. While these pits did not sample the entire soil mass traversed by the tree roots, they provided a measure of the soil conditions in the immediate neighborhood of each tree and permitted a comparison of the tree locations within the stand.

Examination of profiles in the nine pits showed the A_{00} and A_1 layers to be quite uniform in thickness, approximately 1 inch and 2 inches respectively. A diagram of the soil profile, with the ranges of variation, is shown in Figure 2.

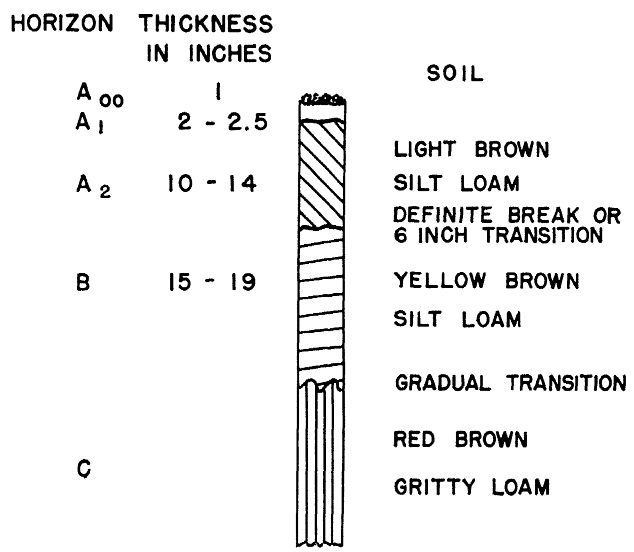


Fig. 2.—Stylized profile of Wooster silt loam under eastern white pine, Compartment K2, Secrest Arboretum, Wooster, Ohio.

The A_2 layer ranged from 10 to 14 inches in thickness and consisted of a light brown, silty loam with occasional small sandstone and shale fragments. While the transition from A_1 to A_2 was distinct, that between A_2 and B was variable both in depth and in clarity. In two pits, for example, the 12-inch deep A_2 showed an abrupt interface with the B horizon. In two other pits, an A_2 of 9 inches, beneath which lay a 6-inch transition zone, merged gradually into the B horizon. The B consisted of a yellow-brown silt loam and contained an increasing number of shale and sandstone particles with increasing depth.

The transition from B to C was quite indefinite, with the soil in this lowest horizon tending towards a brownish, gritty loam with increasing depth. Clay content appeared to increase with depth. The rounded lumps of sandstone and shale increased in size and frequency at the deeper levels, while occasional pockets of gravel were encountered at all depths.

Root development was concentrated in the A_1 and upper 3 to 4 inches of the A_2, although a few roots were present to the bottom of the deepest pit, approximately 5.5 feet. In all cases, markedly thicker lateral roots had been developed on the uphill side of the tree, particularly in the upper 8 to 10 inches of soil.

Three 3-inch core samples were taken from A_2, B, and C horizons in each pit, giving a total of 81 core samples (nine samples per horizon per tree locale). Soil trimmed from core samples was used for bulk samples. In the laboratory, the cores were soaked in water for 2 days and then placed in a pressure chamber at one-third atmosphere pressure for 3 days. Field capacity was calculated as bulk density of the soil multiplied by percent by weight of moisture remaining in the soil on removal from the pressure chamber.

Bulk samples were lumped together by horizon within each pit and this composite sample was ground and mixed thoroughly. Wilting point was determined for the A_1, A_2, B, and C horizons in each pit, using a pressure membrane cell and converting to volume of water. Thus, in the area adjacent to a tree, each of the four horizons was sampled nine times. Field capacity and wilting point data are summarized in Table 2.

The volume of available water per foot of soil in each horizon was obtained by the difference between field capacity and wilting point. Total soil storage was calculated by multiplying available water in the horizon by the horizon depth in feet (Table 3). No data were obtained for available water in A_1 horizon but an arbitrary value of 150 percent of the A_2 value was assigned to this horizon. It was assumed that root occupancy in A_1, A_2, B, and C horizons was 100, 100, 90, and 70 percent, respectively.

The attainable water (that which tree roots actually encounter) was estimated by multiplying available water in a horizon by the appropriate root occupancy. Total attainable water in the root zone amounted to 7.4 inches, while total soil storage in the root zone was 8.7 inches.

TABLE 2.—Summary of Field Capacity and Wilting Point Data for A_2, B, and C Horizons Expressed as Inches of Available Water per Foot of Soil. Each Figure Is the Mean of Three Observations Except as Noted.

Tree No.	Pit	Field Capacity A_2	Field Capacity B	Field Capacity C	Wilting Point A_2	Wilting Point B	Wilting Point C
1	A	3 2	3.2	3.4	0.62	1.76	1.85
	B	3 2	3.3	3.4	0.75	1.65	1.86
	C	3 3	3.3	3.5	0.65	1.54	1.76
2	D	3.3	3.5	3.1	1.12	1.99	1.77
	E	3 2	3.4	3.1	0.97	1.84	1.64
	F	3 2	3.5	3.0	1.26	1.98	1.96
3	G	3 2†	3 2*	3.1	0 92†	1.92†	1.86†
	H	—	—	3 2	—	—	1.89
	I	3 1*	3.6†	3.5	1.31†	2.00†	1.86†

*Mean of four observations.
†Mean of five observations.

COMBINATION OF SOIL AND WEATHER DATA TO OBTAIN PERIODIC MOISTURE DEFICITS

Available soil storage, calculated as described in the previous section, was needed to compute daily moisture deficits. A computer program developed by Zahner and Stage (43) to obtain deficit values requires knowledge of the following variables:

- Daylength at the test latitude expressed as a percentage of a 12-hour day.
- Daily rainfall and maximum and minimum temperatures for 365 days per year, with February 29 omitted from each leap year.
- A mathematical function to express realistic soil moisture depletion for the soil under consideration, based on total soil storage and soil texture.
- Estimates of available soil moisture for various periods of the year or growing season.

Moisture deficit is the difference between potential evapotranspiration and moisture removed from the soil, while the rate and amount of water removed is a function of the volume of water in storage and potential evapotranspiration. Thornthwaite's (36) equation was used in the computer program to calculate potential evapotranspiration.

Daily weather observations for the period January 1, 1912 to December 31, 1961 were obtained

TABLE 3.—Summary of Soil Water Storage and Attainable Water Data.

Variable	A_1	A_2	B	C
Wilting point in /ft. soil	—	0.9†	1.8†	1.8‡
Field Capacity in./ft soil	—	3.2*	3.4*	3 2*
Available water in./ft. soil	3.5	2.3	1.6	1.4
Horizon depth in feet	0.17	1.00	1.42	2.50
Water in horizon	0.60	2.30	2.27	3.50
Total soil storage		8.7		
Root occupancy as percent of horizon	100	100	90	70
Attainable water in. per horizon	0.6	2.3	2.0	2.5
Attainable water in total root zone		7.4		

*Mean of 27 observations
†Mean of 29 observations
‡Mean of 31 observations

from the Statistics Laboratory at the Ohio Agricultural Research and Development Center. These consisted of daily maximum and minimum temperatures in degrees Fahrenheit and precipitation in 0.01-inch units. The observations were entered on IBM cards according to standard Weather Bureau practice.

Based on the soil observations summarized in Table 3, a soil moisture depletion curve typical of a loam soil with a total storage capacity of 8 inches was used in computing cumulative and daily moisture deficits. Although the program computes several other deficit values, only daily cumulative moisture deficits were used in this study.

Cumulative moisture deficits were selected for five periods during any two successive growing seasons as being those most likely to have a significant effect on tree growth during a single growing season.

Since the growing season in central Ohio extends from mid-April to early October, moisture deficits were calculated for the period March 1 to October 31 to fully cover the growing season. This was done for each year, producing two external variables: total deficit in the current growing season and total deficit in the previous growing season.

The August-October period in the previous year was included since conditions in this period may permit accumulation of food materials and influence growth in the subsequent growing season.

For the current year, the June-August period was chosen as most likely to affect termination of shoot elongation. The latter limits cambial development by reducing the flow of carbohydrates and growth regulating substances from the apical regions and needles of the upper crown (39).

The September-October period in the current year was included to cover the possibility that growth might extend into this period to a greater extent than supposed.

The March-May period in the current growing season was not included since moisture is seldom a limiting factor during this period at Wooster.

Thus, the five growing season moisture deficit periods were:

1. March 1 to October 31, previous year.
2. August 1 to October 31, previous year.
3. March 1 to October 31, current year.
4. June 1 to August 31, current year.
5. September 1 to October 31, current year.

The cumulative deficit for each period was read from the computer print-out and used in analyses as an independent moisture deficit variable.

COLLECTION, PREPARATION, AND EXAMINATION OF WOOD SPECIMENS

FIELD WORK

The site from which the three 52-year-old sample trees were cut in March 1962 sloped down from east to west. All three trees showed considerable compression wood development on the western side of the stem. It was decided that, while a greater variation in shrinkage would certainly be found on comparing east and west radii, samples from the north-south diameter would give a more accurate picture of normal development. For this purpose, compression wood was regarded as an abnormal wood form, although it was recognized that few conifers attain merchantable size without the presence of some compression wood.

To minimize the effect of annual branch whorls on the wood properties of the specimens, a sample section 0.5 foot long was cut from the middle of each internode. When a complete series had been assembled to represent each year's growth, the sections were placed in polyethylene bags and stored at —15° C.

LABORATORY WORK

To achieve a balance between the amount of work which was feasible while providing observations along the entire stem, it was decided to sample every 4th internode beginning with the 2nd internode from the tip, i.e., 2, 6, 10, 14, etc. A total of 12 internodes were sampled, with the smallest having 2 growth rings and the largest 46.

The selected 0.5 foot stem sections were cut transversely to give:

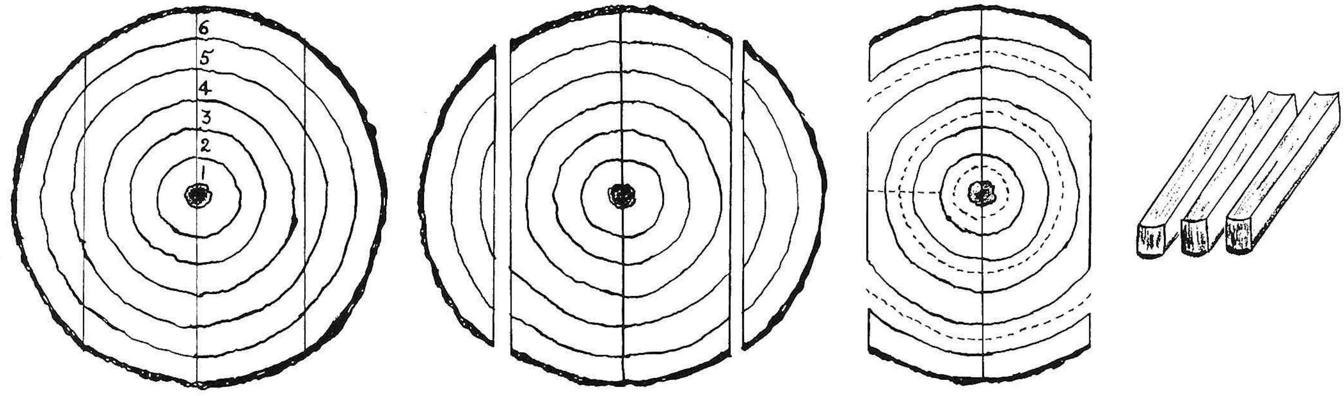
- One 0.5-inch thick section providing material for cell number and ring width measurements.
- One 5.5-inch thick section providing material for specific gravity and longitudinal shrinkage analyses.

All physical measurements were taken at 21° C. and a relative humidity of 25 to 35 percent.

Cell Number and Ring Width

To prepare a specimen for ring width measurement, a north-south diameter was drawn through the pith of the 0.5-inch thick sample, which had been soaked in water overnight. An area along this diameter was trimmed with a scalpel, giving a clean surface for microscopic examination. The cleaned surface was stained with a weak safranin solution, making the cell walls easily visible under the microscope.

The block was mounted on a moving stage based on the design by Echols and Baldwin (11), with movement recorded by means of a Starrett dial gauge reading in 0.001-inch units. By observing the moving surface through a microscope, with a crosshair eye-



(A) (B) (C) (D)

Fig. 3.—Diagram of cross-section showing north-south radius and parallels (a), slabs cut away (b), dotted path of saw in separating annual rings (c), and three specimens from an annual ring (d).

piece at 125x magnification, it was possible to count the number of earlywood and latewood cells along each radius and to measure the widths of the respective bands.

Mork (23) defined a latewood cell as one where twice the width of the common cell wall, in the radial direction, is greater than the cell lumen. This definition of latewood was used throughout the study.

To obtain the distance from the center of the pith to the edge of the first growth ring, the diameter of the entire first year's growth was measured and divided by two.

Two readings were made along both radii. In subsequent analyses, data representing number of earlywood cells, number of latewood cells, and widths of these zones were averages of the two observed measurements. Percentage of latewood was calculated from mean latewood width and mean total ring width.

Longitudinal Shrinkage

Specimens for shrinkage measurements were cut from the 5.5-inch thick section in the following manner. A north-south diameter was drawn through the pith on the transverse face of the section and lines parallel to this were marked 2 inches on each side of the diameter (Figure 3). The peripheral portions of the block were removed by sawing along the outside parallels.

Even-numbered growth rings from the pith were cut from the central block by sawing tangentially through the intervening growth rings. Three specimens were split from each of these plates, giving specimens with fiber direction parallel to the long axis. Each specimen was trimmed to consist solely of the desired growth ring and cut to approximately 2 inches in length (2 ± 0.06 inches). The specimens were placed in identified cheesecloth bandoliers in deionized water to await measurement.

Three specimens were cut from each 2nd ring on a north-south diameter at 12 levels in the stem. This resulted in 864 specimens from each tree or a total of 2592 specimens from the three stems.

The length of each specimen was measured in the green and oven-dry condition, using the apparatus shown in Figure 4. Divisions on the gauge allowed measurement to 0.0005 inch.

After the green measurement, the specimens were allowed to reach approximately 12 percent moisture content by standing over a saturated sodium bromide solution. Then the specimens were placed in an oven at 105° C. for 16 hours. Next the specimens were

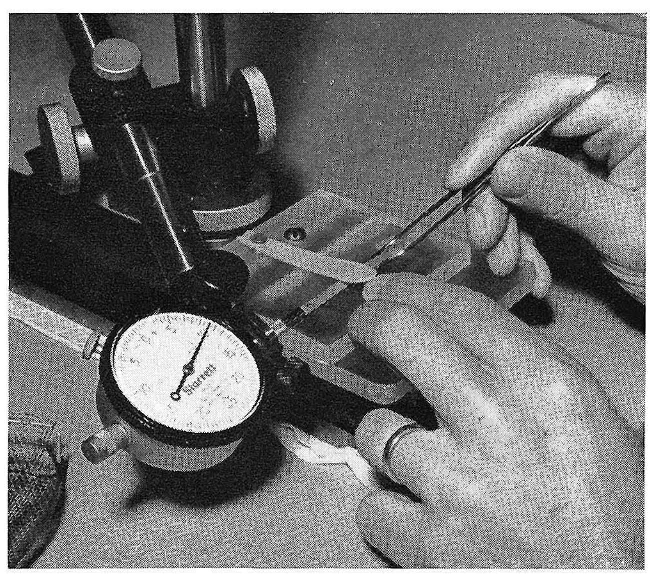


Fig. 4.—Device used to measure longitudinal shrinkage with specimen being placed in position.

put into a desiccator over 'Drierite," a commercial desiccant containing calcium sulphate, and allowed to cool to room temperature

Specimens were removed individually through a small aperture in the desiccator cover and weighed to the nearest 0.001 gram to obtain oven-dry weight. After weighing, oven-dry length was obtained with the apparatus noted above.

Longitudinal shrinkage was obtained from the difference between green and oven-dry lengths and expressed as a percentage of oven-dry length:

$$\text{Longitudinal Shrinkage Percent} = \frac{\text{Green Length} - \text{Oven-Dry Length} \times 100}{\text{Oven-Dry Length}}$$

In the present study, oven-dry length was used as the base, although shrinkage frequently is calculated as a percentage of the green dimension. The actual comparative base was not of great significance except that it had to be consistently observed throughout the study, since the values obtained were used essentially for comparative purposes. This study was primarily concerned with the relationship existing among the values from various positions in the tree, rather than with the absolute values.

Values were obtained for three specimens from each growth ring. These were averaged and the mean used in subsequent analyses. Only total shrinkage, from the green to the oven-dry state, is discussed in this paper.

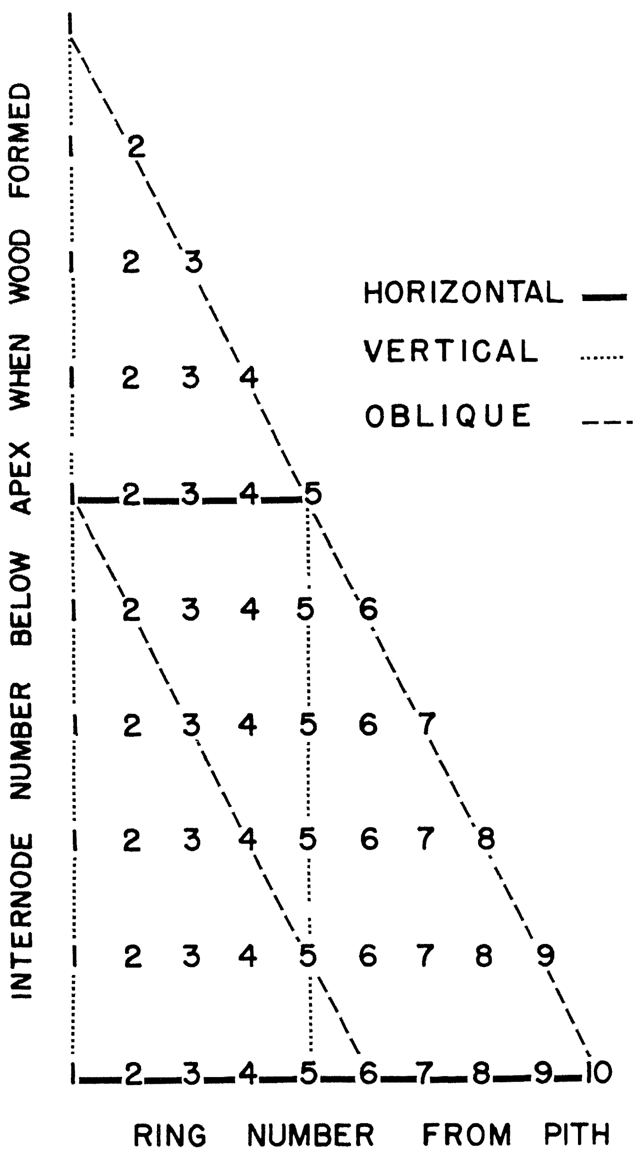


Fig. 5.—Diagram showing three sequences in which annual ring observations may be grouped.

Specific Gravity

The shrinkage specimens were used to determine specific gravity for the individual growth rings. Immediately following weight and length measurements of each oven-dry specimen, the block was impaled on a dissecting needle and totally immersed in a graduate cylinder partially filled with mercury. The cylinder was graduated in 0.1 ml. units and, by means of a burette magnifier, the level of the meniscus was read to 0.01 ml. Oven-dry volume of each specimen was obtained by direct reading of the mercury level displacement. Specific gravity was calculated as:

$$\text{Specific Gravity} = \frac{\text{Oven Dry Weight of Block (g)}}{\text{Volume of Mercury Displaced (ml)}}$$

Specific gravity may be calculated either on a green or an oven-dry volume basis. Oven-dry volume was used in this study as it was more convenient to obtain and was more desirable, since the specimens were to be analyzed spectrographically later.

Values were obtained for three specimens from each growth ring. These were averaged and the mean used in subsequent analyses.

ARRANGEMENT OF STEM OBSERVATIONS

Since the observations were recorded in terms of entire growth rings at various heights in the stem, they were considered in the manner reported by Duff and Nolan (10). Data collected at several distances from the pith and heights in the stem are compared along three major axes termed oblique, horizontal, and vertical (Figure 5).

The oblique sequence, describing variation from top to bottom of a stem within the growth sheath laid down in a given year, shows change due to position in the stem. This may be measured in terms of physiological or physical intervals from the current stem apex. This sequence therefore eliminates variation due to differences in growing seasons since all of the material examined grew in the same season.

The confounding effect of environmental differences is not avoided entirely because the size of a large tree precludes its existence within a wholly uniform environment. However, throughout this study it was assumed that all wood comprising a given growth sheath was formed under the same environmental conditions. While annual environmental variation is minimized in examining data within a single oblique sequence, comparison of one oblique sequence with another provides a means of estimating the effect of annual environmental differences on the pattern resulting from position in the stem.

The horizontal sequence applies to observations of successive rings from the pith along a pith-circumference radius at a given height in the stem. This is the sequence which has received the greatest attention historically, primarily because it is most easily observed. It is useful in comparing wood properties over a period of years at a specified height in the stem.

Changes between points along the horizontal sequence may be due to increasing age of the cambium, the ever-increasing distance between the sampling level and the stem apex, and yearly variation in temperature, soil moisture availability, and other variable factors comprising the environment. Thus, in this sequence the influences of environmental factors are confounded with those of factors intrinsic to the tree.

In oblique sequences for different growth sheaths, the relationship between values obtained at the 1st and 2nd internodes below the stem apex is persistent for a given wood property. This is also true for the 2nd and 3rd internodes, the 3rd and 4th, and progressively down the stem. Thus a substantially predictable relationship exists between internodal values within an oblique sequence curve, and this relationship is relatively constant among such curves or growth sheaths representative of different growing seasons. Such families of curves have been demonstrated for ring width in red pine (10) and for tracheid length and wood density in Corsican pine (28).

While the relationship between a pair of internodal values (for example, 2nd and 6th below the apex) may be relatively constant in several growth sheaths, the actual values of the observations in the various sheaths may differ considerably.

In Figure 5, the values comprising the horizontal sequence at the 5th internode below the tree apex are values from 5 successive growth sheaths.

Given the ratio between internodal values in oblique sequences discussed above, one would expect to find the horizontal and oblique sequences for the first 5 rings from the pith and for the first 5 internodes from the tree apex similar in general form. Greater variation would exist in the horizontal sequence, since it is composed of material created in 5 different growing seasons. Thus horizontal and oblique sequences incorporating identical numbers of rings from the pith and internodes below the stem apex should show similarity of form.

The horizontal curve would show greater variation between individual values for properties markedly affected by the environment than for properties relatively independent of a protean environment. Comparison of these two sequences for a given property

TABLE 4.—Average Value (m) and Standard Deviation (s) of Dependent Variables by Tree and Pooled.

Variable		Tree 1	Tree 2	Tree 3	Pooled
Specific gravity	m	0.341	0.372	0.345	0.353
	s	0.036	0.035	0.032	0.037
Shrinkage percent	m	0.23	0.20	0.23	0.22
	s	0.13	0.09	0.12	0.12
Earlywood cells	m	93.0	95.3	104.9	97.7
	s	48.9	38.8	37.1	42.2
Latewood cells	m	4.8	5.6	3.6	4.7
	s	2.7	3.6	2.1	3.0
Total cells	m	97.8	100.9	108.5	102.4
	s	49.4	38.5	36.9	42.2
Earlywood width in inches	m	0.141	0.137	0.162	0.147
	s	0.072	0.049	0.051	0.059
Latewood width in inches	m	0.003	0.004	0.003	0.003
	s	0.002	0.003	0.002	0.002
Total ring width in inches	m	0.144	0.140	0.164	0.150
	s	0.071	0.049	0.051	0.059
Percentage of latewood	m	2.54	2.62	1.69	2.28
	s	1.72	1.69	1.12	1.59

illustrates the extent to which an attribute is affected by factors outside the tree.

Within each 3rd or vertical sequence, values are compared of wood laid down by cambium of the same physiological age as measured from the pith but at different heights in the stem and during a succession of growing seasons (for example, a comparison of values of the 5th ring from the pith in all internodes 5 years of age or older). Since cambial age is held constant, this sequence illustrates the effect of environmental changes on meristems of the same physiological age and the same physiological distance below the stem apex, but at an ever-increasing distance above ground level. Therefore, variation is determined primarily by environmental factors, as opposed to the oblique sequence from which yearly weather and similar variables are removed.

Horizontal sequences are discussed in terms of the number of rings from the pith and oblique sequences are described in numbers of internodes below the current stem apex. Figure 5 shows that for each oblique growth sheath, the stem apex is at a different level above ground. Therefore, the term current stem apex refers to the stem apex existing at time of formation of any given growth sheath or oblique sequence. When the top of the felled sample tree is used as a point of reference, as in the vertical sequences, it is identified as the final stem apex.

Thus all sample positions are identified in terms of temporal or physiological units, either annual rings or annual internodes, and not in linear units.

As noted above, observations were recorded at 12 levels in the three stems, with values obtained for all even-numbered rings from the pith along a north-south diameter. To obtain a general pattern of development in white pine, it was desirable to treat the three stems as block replications within a single population.

The mean value and standard deviation for each physical variable were found by tree and for pooled observations from the three trees. The means and standard deviations, shown in Table 4, indicated that the data were sufficiently uniform to permit treating the three stems as a single population. In all analyses, therefore, data for a given locus represent the mean of north and south observations from three trees at the location specified.

Regression Analyses

The present observations were analyzed with the step-wise regression program developed by Westerveldt (41) for use with the IBM 7090 computer. Since specific gravity and longitudinal shrinkage were measured only on the even-numbered rings from the pith and cell number and ring width were observed for every ring, the physical data were treated as two series with different values for the number of observations, N. In analyses involving the first two variables, the number of observations possible per aspect per tree was 144 or a total of 864 for the three trees. Due to missing data at eight locations, the actual number of observations in the analyses was 856.

There were 72 observations involving the pith which consisted of total ring width but with no total cell measurements. These would have required a separate series of analyses on total ring width alone, without direct relation to cell number, width of early-wood or latewood bands, or percentage of latewood. It was decided that the additional work involved would not produce a commensurate increase in information. So these 72 observations were excluded. The number of observations used in the pooled data analyses of cross-section variables was 1728—72=1656.

The pooled data were tested using linear, quadratic, and reciprocal functions of the in-stem independent variable, alone and in association with linear functions of the five soil moisture deficit variables (Table 5). Functions X_1 to X_{13} represent vertical and horizontal positions in the stem, while X_{14} to X_{18} are periodic soil moisture deficit values. The interactions tested between in-stem position and soil moisture deficit are shown by X_{19} to X_{30}.

In all instances it was found that the number of internodes from the apex accounted for slightly more of the variation due to vertical position than did dis-

TABLE 5.—Functions of Independent Variables Tested in Regression Analyses.

	Position in Stem	Interactions			
X_1	Aspect				
X_2	Number of internode from apex	X_{19}	X_2	x	X_{15}
X_3	(Number of internode from apex)^2	X_{20}	X_2	x	X_{16}
X_4	(Number of internode from apex)$^{-1}$	X_{21}	X_2	x	X_{17}
X_5	Number of feet from apex	X_{22}	X_5	x	X_{15}
X_6	(Number of feet from apex)^2	X_{23}	X_5	x	X_{16}
X_7	(Number of feet from apex)$^{-1}$	X_{24}	X_5	x	X_{17}
X_8	Number of ring from pith	X_{25}	X_8	x	X_{15}
X_9	(Number of ring from pith)^2	X_{26}	X_8	x	X_{16}
X_{10}	(Number of ring from pith)$^{-1}$	X_{27}	X_8	x	X_{17}
X_{11}	Number of inches from pith	X_{28}	X_{11}	x	X_{15}
X_{12}	(Number of inches from pith)^2	X_{29}	X_{11}	x	X_{16}
X_{13}	(Number of inches from pith)$^{-1}$	X_{30}	X_{11}	x	X_{17}

Soil Moisture Deficit

X_{14}	Previous year, March 1 to October 31
X_{15}	Previous year, August 1 to October 31
X_{16}	Current year, March 1 to October 31
X_{17}	Current year, June 1 to August 31
X_{18}	Current year, September 1 to October 31

tance in feet from the apex. Similarly, the number of rings from the pith was a more definitive measure of horizontal distance than was inches from the pith. Therefore, variation within the stem is considered in terms of rings from pith and internodes from apex.

In discussing each dependent variable, the equation accounting for the greatest amount of variation is presented. For number of earlywood cells per growth ring and total ring width, the equations do not adequately describe conditions within the ten rings closest to the pith, since none of the tested equations described a sigmoid curve. Beyond the 15th ring, however, the expressions show the changes to be expected with increasing distance from the pith and illustrate the relationships between various levels in the stem.

Changes in longitudinal shrinkage, specific gravity, and percentage of latewood are shown adequately by curves computed from the equations for these variables.

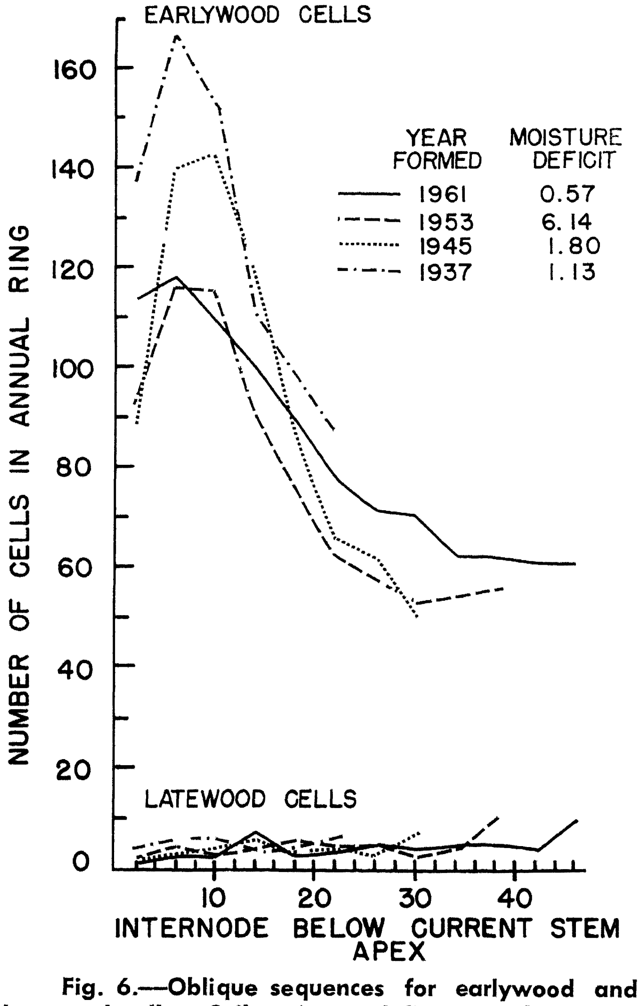


Fig. 6.—Oblique sequences for earlywood and latewood cells. Soil moisture deficit in inches is for current March 1 to October 31.

RESULTS

Number of Cells in Growth Ring

As described above, the number of cells in a growth ring was determined along a north-south diameteron transverse sections at 12 levels, each four internodes apart in each of the three stems. Two stages of tracheid development were recognized and designated earlywood and latewood. The separation was made on the basis of Mork's (23) definition which states that a latewood cell is one where twice the width of the common tangential cell wall, measured in the radial direction, is greater than the cell lumen.

This definition was made for use with Norway spruce and is effective for this wood. It leaves something to be desired, however, in the case of eastern white pine. In the latter, there is a gradual change from early to late cell type, with a progressive color and shape change spread over several cells. Thus there is a possibility that the physiological boundary between the two forms is not precisely identified by this definition.

Efforts to produce alternative criteria which would define the transition zone in objective, reproducible terms were unsuccessful, however. So the Mork definition is used with the reservation that, for eastern white pine, it is the best usable definition rather than the best physiological definition.

As shown in Figures 6 and 7, earlywood tracheids predominate in the growth ring. The average number per annual ring was 98 and ranged from 24 to 244. The average number of latewood cells varied between 1 and 23, with the average 5.

Four oblique sequence curves are shown in Figure 6 with the soil moisture deficit for the March 1-October 31 period of the year in which the sheath was formed. This particular periodic soil moisture deficit is shown since, of the five deficits tested, regression analysis indicated it to be most closely related to earlywood formation. The curves ascend to approximately the 8th internode below the current stem apex. After that they decline rapidly at first and then more gradually with increasing distance from the apex.

Latewood tracheid sequences show a gradual, although small, increase in number of cells with progression down the sheath. There is a visible, repetitive pattern in relation to the current stem apex. Although the absolute values along the curves vary, the relative position of one value to another within a given growth sheath is largely predictable.

Variation with a fluctuating environment is evident in the horizontal sequence curves in Figure 7, representing change from pith to periphery at the 10th, 22nd, 34th, and 46th internodes below the final stem apex. There is a marked rise and fall between

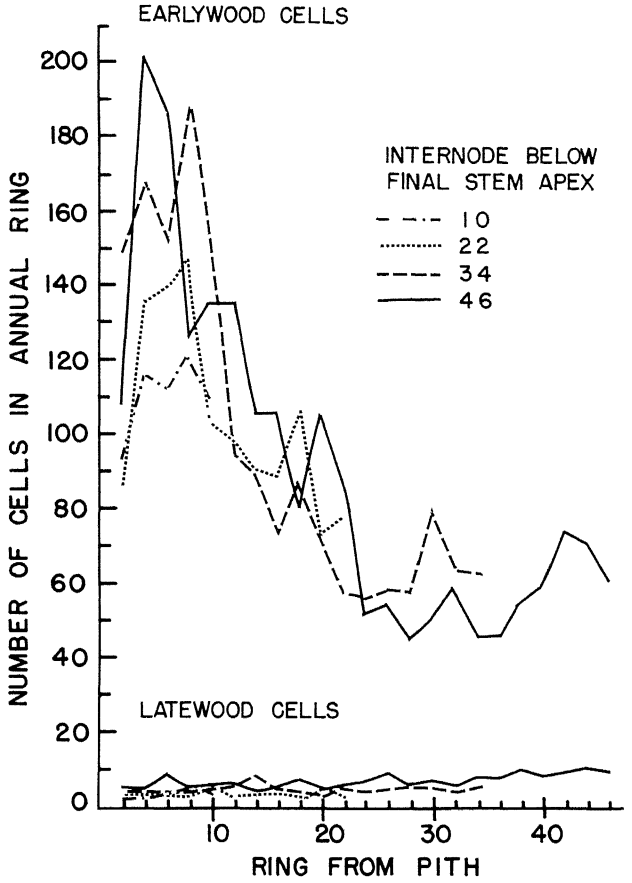


Fig. 7.—Horizontal sequences for earlywood and latewood cells.

the 2nd and 10th rings from the pith and, although the curves tend to level off or even ascend beyond the 35th ring from the pith, divergencies are substantial.

Both the horizontal and oblique sequences, in effect, represent variation with distance from the current stem apex. The difference is that all values within the oblique sequence were formed in the same growing season, while in the horizontal sequence each value was formed in a different growing season. The earlywood obliques are smoother in outline than the horizontals, as expected for an attribute markedly affected by a changeable environment. Latewood data provide horizontal curves slightly more erratic than the oblique.

A further illustration of positional and moisture deficit effects is given in Figure 8, showing vertical sequences plotted over year of formation. Each curve represents cambium of a given age with ascending position in the stem.

The two rings close to the pith, 2 and 10, show a general decline in the number of earlywood cells formed with increasing height in the stem, although with a slight increase in the later years (1949 to 1961). The two rings farther from the pith show an upward trend corresponding to that of the rings close to the pith for the same period. Latewood cells show a decline in number with increasing height in the stem. Correspondence with moisture deficit is not marked in either case.

Cell number observations were analyzed by stepwise regression and combinations of the independent variables shown in Table 5 were tested in turn. For earlywood cells, the best estimate of association was obtained with the equation given below, which had a coefficient of determination (R^2) of 0.663, i.e., the variables in the equation accounted for 66 percent of the total variation in number of earlywood cells formed in growth ring, with a standard error of estimate of $\pm$ 24.6.

$$Y = 137.302 + 2.842X_2 - 0.0332X_3 - 6.980X_8 + 0.0928X_9 - 0.0622X_{16}$$

where:

X_2 = internode from apex
X_3 = (internode from apex)^2
X_8 = ring from pith
X_9 = (ring from pith)^2
X_{16} = current year deficit, Mar. 1 to Oct. 31.

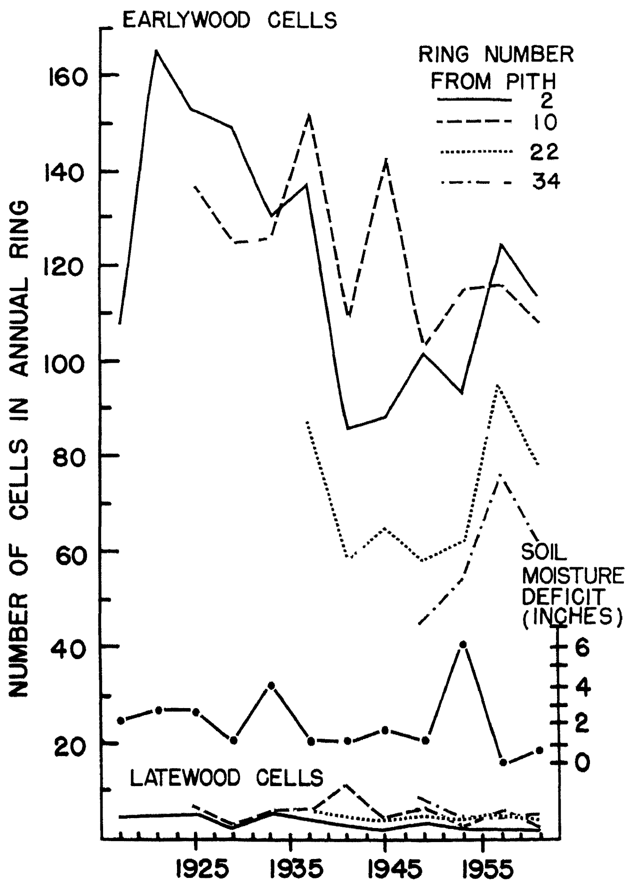


Fig. 8.—Vertical sequences for earlywood and latewood cells arranged over year of wood formation and current March 1 to October 31 soil moisture deficit.

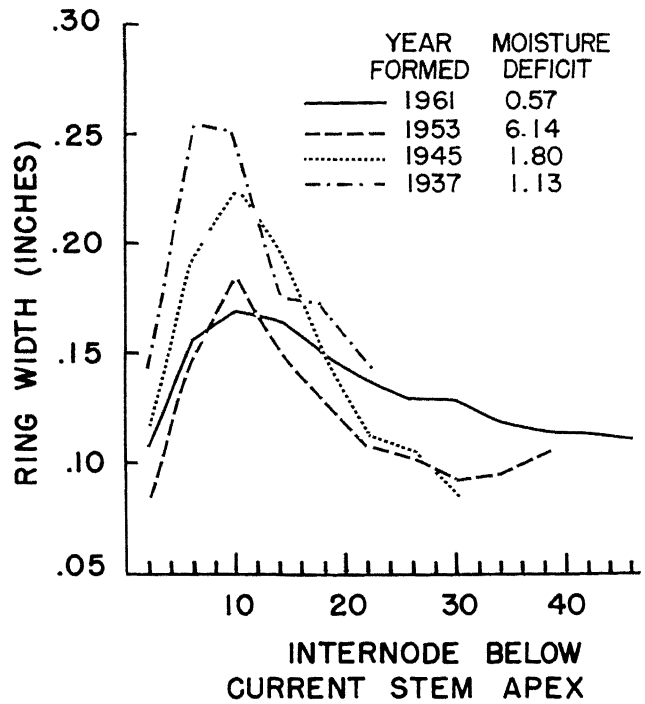


Fig. 9.—Oblique sequences for ring width. Soil moisture deficit in inches is for current March 1 to October 31.

To estimate the relative importance of the individual variables, a "t" value was calculated for each one as:

$$t = \frac{\text{partial regression coefficient}}{\text{standard error of the coefficient}}$$

A value of 32.266 was obtained for ring from the pith (X_3), 18.525 for current deficit (X_{16}), and 9.308 for internode from the apex (X_2). Thus, within-stem position was of considerably greater importance than moisture deficit in determining the number of earlywood cells formed, although all three were significant at the 1 percent level. This relative importance is apparent from the curves in Figures 6 and 7. The low value for internodes from apex (X_2) was probably due to the nature of the calculations which grouped all ring values at a given internode, thus reducing the sensitivity of the variable.

An analogous regression of latewood cell number data proved quite ineffective, the best estimate giving $R^2 = 0.115$ with a standard error of $\pm$ 2.8. No equation is given for latewood cells, since apparently factors affecting latewood cell formation were sampled inadequately in the study.

Ring Width

Comparison of the oblique sequences for ring width (Figure 9) with those for number of earlywood cells (Figure 6) illustrates the close relationship which must exist between the two properties since earlywood cells form the majority of the growth ring. The high correlation of number of earlywood cells in the growth ring with total ring width, + .91, indicates that increase in ring width was due principally to greater production of earlywood tracheids by the cambium in a wet year than in a dry year, rather than to the formation of an equivalent number of larger cells. There may have been a slight accompanying increase in tracheid diameter, however.

Ring width was virtually independent of variation in the number of latewood cells formed, the correlation coefficient being —.01. As with number of earlywood cells, ring width proved to be most closely related to total current moisture deficit of the five deficits tested.

Comparison of the oblique sequence curves in Figure 9 repeats the form discussed with regard to earlywood formation. The inherent pattern was repeated of rapid increase from the apex to the 8th or 10th internode below the current stem apex, followed by a decline in width to the base of the growth sheath. Absolute values at a given distance from the current apex in the several curves varied with increasing age of the tree, with the curves tending to become flatter. However, the relationship between specific internodes was quite similar in different growth sheaths.

Four horizontal sequence curves representing internodes 10, 22, 34, and 46 below the sample tree

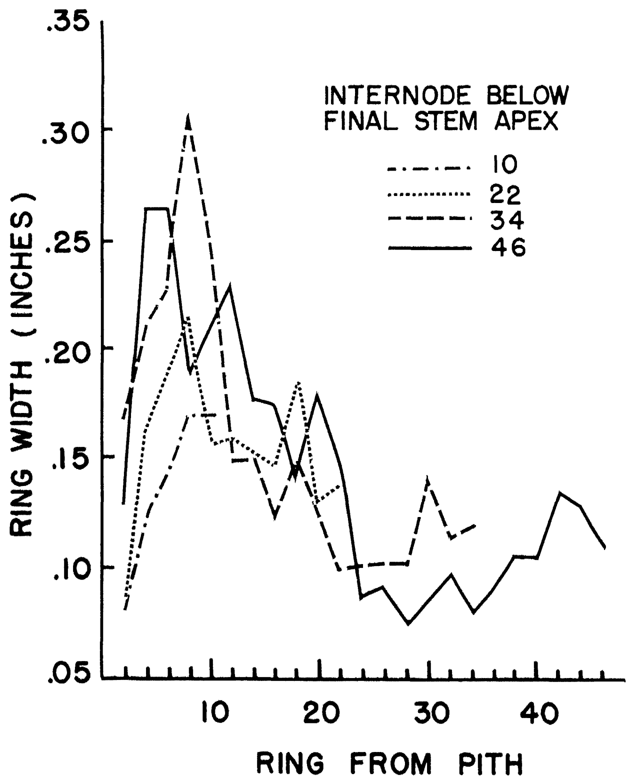


Fig. 10.—Horizontal sequences for ring width.

stem apex are shown in Figure 10. They show an increase in width to approximately the 8th ring from the pith, followed by a progressive but somewhat erratic decrease in width outwards to about ring 28. Ring width thereafter tended to increase to the circumference.

The general pattern of the curves is similar to that for the oblique sequences. However, there is greater irregularity among the values along a given curve, as might be expected for material susceptible to seasonal changes and laid down under different growing conditions.

Vertical sequence curves are shown in Figure 11, with the curves arranged above year of formation. The influence of a changeable environment, including soil moisture deficit, is evident. There was a trend of decreasing ring width with increasing height in the stem for rings closer to the pith, except during the last 12 years illustrated, and of decreasing ring width with increasing horizontal distance from the pith.

Regression analyses of the observations showed that the independent variables making up the following equation accounted for 42 percent of the total variation in ring width ($R^2 = 0.423$, with a standard error of estimate of $\pm$ 0.0449 inch).

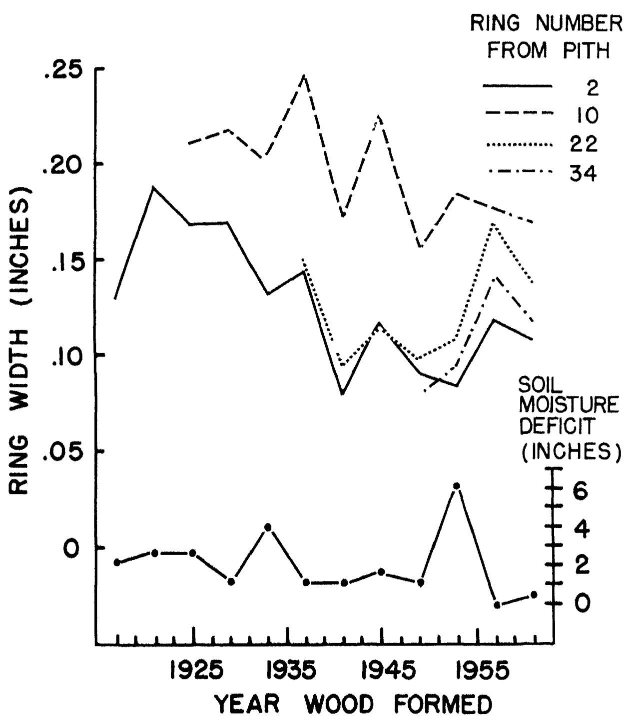


Fig. 11.—Vertical sequences for ring width arranged over year of wood formation and current March 1 to October 31 soil moisture deficit.

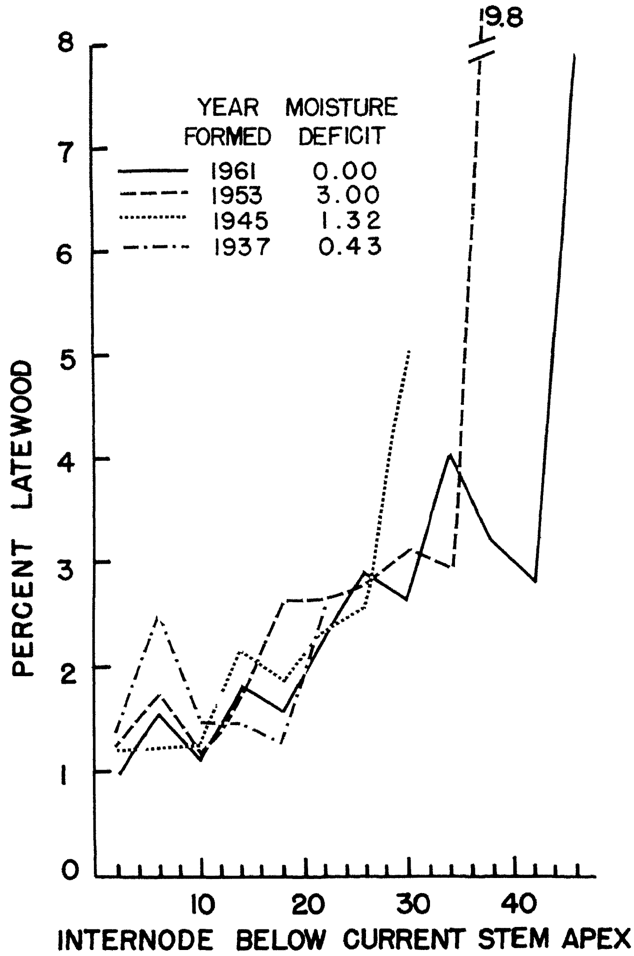


Fig. 12.—Oblique sequences for percentage of latewood. Soil moisture deficit is for current June 1 to August 31.

$$Y = 145.718 + 5.527X_2 - 0.0664X_3 - 5.760X_8 + 0.0515X_9 - 0.106X_{16}$$

where:

X_2 = internode from apex
X_3 = (internode from apex)^2
X_8 = ring from pith
X_9 = (ring from pith)^2
X_{16} = current year deficit, Mar. 1 to Oct. 31

In calculating "t" for the independent variables, values were obtained of 9.983 for internode from apex (X_2), 14.689 for ring from pith (X_8), and 17.483 for current deficit (X_{16}). As with number of earlywood cells, ring from pith and moisture deficit accounted for the greatest portion of the variation, with moisture deficit assuming greater importance in ring width determination. Probably this was due to a slight increase in tracheid diameter with increased water availability, accompanying the increase in earlywood cell number.

Percentage of Latewood

Percentage of latewood is the width of the latewood band in a growth ring expressed as a percent-

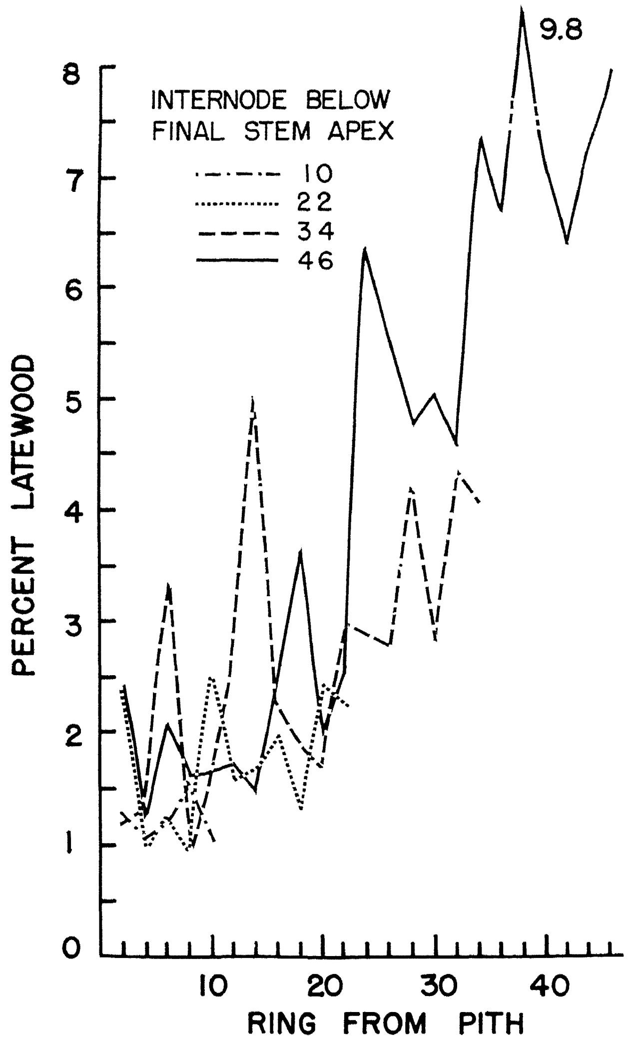


Fig. 13.—Horizontal sequences for percentage of latewood.

age of the entire ring widtn. As has been noted, the number of latewood cells tends to increase slightly with increasing distance from the current stem apex along any growth sheath, while the number of earlywood cells beyond the 8th internode from the apex decreases quite rapidly and then more gradually. Thus, although there is little change in the number of latewood cells, due to the decline in number of earlywood cells the latewood band occupies a progressively greater portion of the growth ring with an increasing number of internodes from the current stem apex. So the latewood band becomes a more potent factor in the characteristics of the ring as an entity.

The oblique sequence curves for percentage of latewood in Figure 12 show clearly the increase in latewood percentage basipetally along a given growth sheath, with the rate of increase rising with successively greater distances from the current stem apex. Variation in association with soil moisture deficit was not particularly evident.

Four horizontal sequences are shown in Figure 13. As with earlywood cells and ring width, these display greater variation within each sequence while adhering to the general ever-steepening form of the oblique sequences.

Unlike earlywood and ring width, percentage of latewood was associated most closely with moisture deficit during the period June 1 to August 31. However, a strong positional influence was exerted over the entire curves, which generally ascend with increasing physiological distance from the pith.

Soil moisture levels are shown in association with vertical sequences in Figure 14. These indicate that while percentage of latewood fluctuates seasonally, it remains relatively constant as a given ring from the pith is followed upwards in the stem. The vertical curves illustrate also the increase in percentage of latewood with increasing number of rings from the pith at a specified level in the stem.

Of the regression equations tested, the following gave an R^2 value of 0.257 and a standard error of estimate of $\pm$ 2.015. Even at this low level, the equation was superior to others tested and was significant at the 1 percent level.

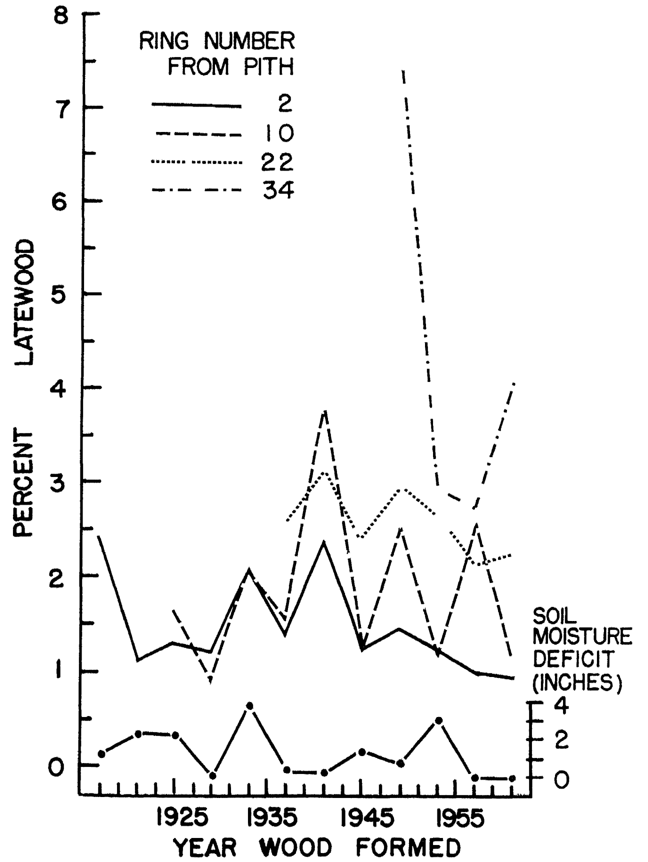


Fig. 14.—Vertical sequences for percentage of latewood arranged over year of wood formation and current June 1 to August 31 moisture deficit.

$$Y = 1.509 - 0.0789X_{17} + 0.00160X_2 + 0.0567X_4 + 0.000895X_9 + 0.00345X_{10}$$

where:

X_2 = internode from apex
X_4 = (internode from apex)^2
X_9 = ring from pith
X_{10} = (ring from pith)^2
X_{17} = current year deficit, June 1 to Aug 31

Individual variable "t" values were calculated and resulted in values of 3.174 for internode from apex (X_2), 3.219 for ring from pith (X_9), and 8.863 for June 1 to August 31 moisture deficit (X_{17}). Thus percentage of latewood appeared to be slightly more closely associated with moisture deficit level than with in-stem position, although all three were statistically significant at the 1 percent level. This effect was probably due to the heightened soil moisture deficit, which reduces the rate at which earlywood cells are formed and promotes conditions favorable for latewood formation.

Longitudinal Shrinkage

Longitudinal shrinkage is expressed throughout in terms of the difference between green and oven-dry length parallel to the grain as a percentage of oven-dry length. Pooled data from the three trees were used to obtain the oblique sequence curves shown in Figure 15. These show a precipitous drop in longitudinal shrinkage between the 2nd and 6th internodes in each growth sheath, from values of 0.7 and 0.8 percent to 0.2 percent. Thereafter there was fluctuation in each sequence, but seldom more than ± 0.05 about 0.2 percent.

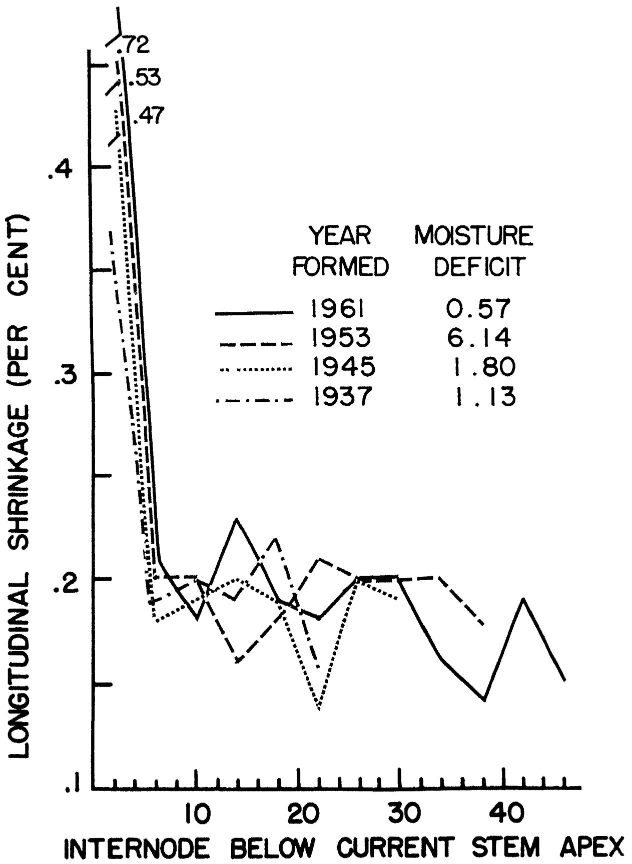


Fig. 15.—Oblique sequences for longitudinal shrinkage. Soil moisture deficit in inches is for current March 1 to October 31.

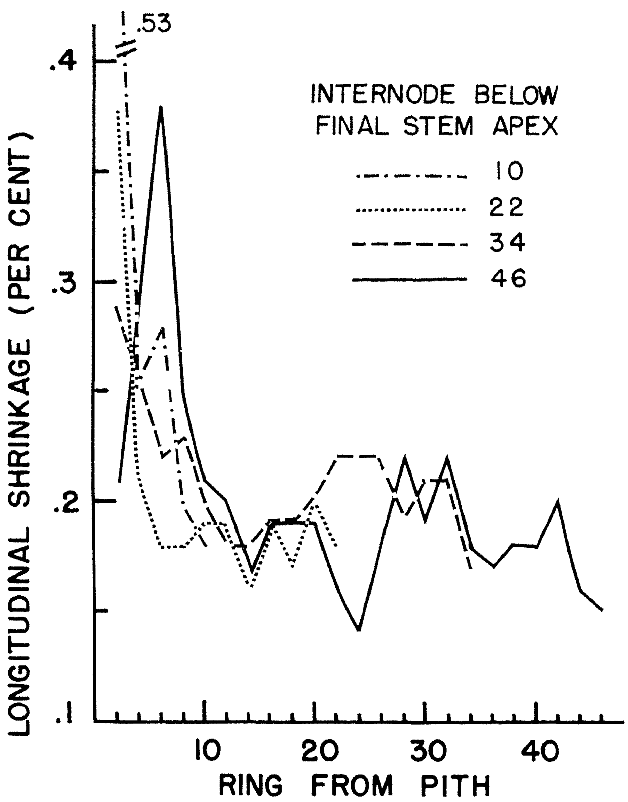


Fig. 16.—Horizontal sequences for longitudinal shrinkage.

There was no visible difference between the sheaths laid down in different growing seasons, with variation in the lower portions of the curves essentially random. This general pattern is repeated in the horizontal curves shown in Figure 16.

In the vertical sequences (Figure 17), there was no discernible pattern associated with soil moisture deficit. Nor was there any tendency for longitudinal shrinkage to increase or decrease within a specific growth ring from the pith with increasing height in the stem. An exception was the 2nd ring from the pith, which showed an upward trend with increasing height in the stem.

Regression analysis gave an equation having $R^2 = 0.237$, with a standard error of the mean of ± 0.106. Highly significant F values were obtained with X_4 and X_{10}. Addition of soil moisture deficits added nothing to the regression analysis in this instance and thus none are included in the equation.

$$Y = 0.116 + 0.00922X_1 + 0.00042X_2 + 0.815X_4 + 0.00044X_8 + 0.306X_{10}$$

where:

X_1 = aspect
X_2 = internode from apex
X_4 = (internode from apex)$^{-1}$
X_8 = ring from pith
X_{10} = (ring from pith)$^{-1}$

Specific Gravity

The oblique sequences in Figure 18 show high specific gravity close to the stem apex, declining to a minimum about the 8th internode and then increasing gradually to the base of the sheath. Moisture deficits are shown for the period March 1 to October 31 in the year the wood was formed. There was no typical difference between sequences for the wettest and the driest years.

The form of the oblique sequences is repeated in the horizontal sequences (Figure 19), which decline to ring 8 or 10 and then increase towards the periphery.

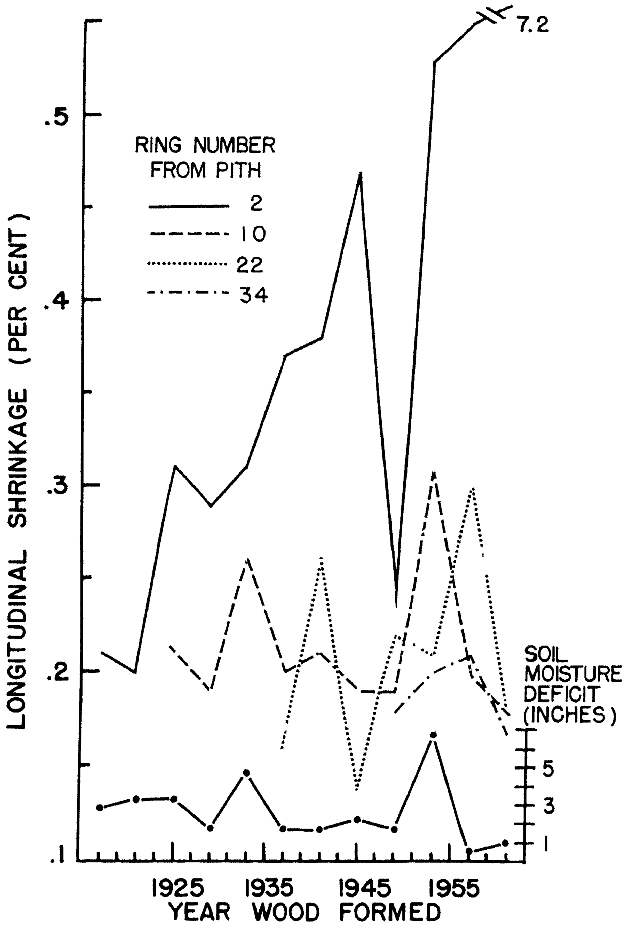


Fig. 17.—Vertical sequences for longitudinal shrinkage arranged over year of wood formation and current March 1 to October 31 soil moisture deficit.

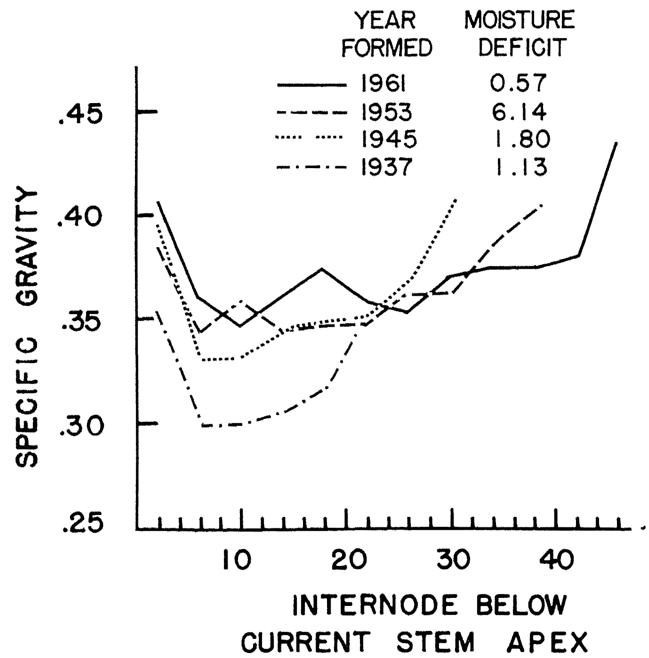


Fig. 18.—Oblique sequences for specific gravity. Soil moisture deficit in inches is for current March 1 to October 31.

The vertical sequences (Figure 20) show a trend of increasing specific gravity with increasing height in the stem for a given ring, particularly for those close to the pith, and an increase in specific gravity with a mounting number of rings from the pith. The high specific gravity close to the pith is reflected in the high level of ring 2 throughout.

Regression analysis indicated that specific gravity variation could be expressed by the following equation:

$$Y = 0.321 - 0.00537X_1 - 0.00104X_2 + 0.0458X_4 + 0.00317X_8 + 0.145X_{10}$$

where:

X_1 = aspect
X_2 = internode from apex
X_3 = (internode from apex)$^{-1}$
X_8 = ring from pith
X_{10} = (ring from pith)$^{-1}$

This equation gave a coefficient of determination of 0.429 and a standard error of $\pm$ 0.028. None of the soil moisture variables tested added significantly to the value of R^2 and therefore were not included.

DISCUSSION

Number of Cells and Ring Width

The oblique sequences in Figure 6 show a predictable pattern of earlywood cell formation within the top 8 to 10 internodes of any growth sheath, indicating a dominating within-stem control. The increase in cell numbers immediately below the apex

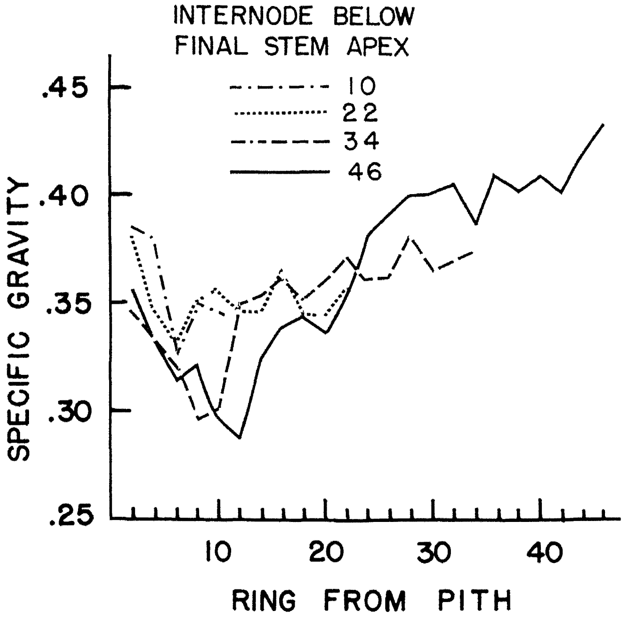


Fig. 19.—Horizontal sequences for specific gravity.

for some 8 internodes was probably due to a progressively increasing flow of carbohydrates and growth regulators into this portion of the stem from the needles and elongating shoots of the uppermost branch whorls.

Below this region, total utilization increases more rapidly than the amount of photosynthate contributed by the needles of the lower branches. Thus, on descending a growth sheath, there is a combination of increasing stem cambial area, a decrease in the amount of food material contributed to the stem cambium by each successively lower branch whorl, and, in the lowest portion of the crown, the possibility of carbohydrate diversion to the branches. When this combination is coupled with increasing distance from the upper crown (the region of greatest carbohydrate and growth regulator synthesis), the result is an ever-diminishing supply of food substances per unit area of cambium with increasing distance from the stem apex. This, in turn, is reflected in a progressive diminution in the number of cells formed on moving basipetally from the 10th internode along a growth sheath.

The production, translocation, and utilization of photosynthate follows approximately the same pattern each year but the level of activity is higher in a wet than in a dry growing season. This association with moisture availability has been demonstrated by Roberts (29), who measured uptake and translocation of $C^{14}O_2$ by yellow poplar seedlings exposed to various levels of water stress. He showed that increased internal water stress reduced both uptake of $C^{14}O_2$ and translocation from the treated leaf.

A similar decrease in the flow of carbohydrates to the cambium in white pine would result in reduced cambial activity and the formation of fewer tracheids. Similarly the flow of auxin to the cambium would be reduced by the effect of increased water stress on stem and needle elongation (16, 22), with a reduction in the enlargement of cambial derivatives and developing tracheids. These consequences are in agreement with Bannan's (1) findings that in *Pinus strobus* an inverse relationship exists between ring width and tracheid length for ring widths greater than 1.0 mm., as were all of the rings in the present study.

To these indirect effects of high soil moisture deficit and resultant increased water stress in the tree, the direct effect of moisture stress on the cambium and maturing tracheids must be added. Reduced cell turgor decreases the frequency of mitosis and stunts cell enlargement, as shown by Ordin (25) working with *Avena* coleoptile.

If the soil moisture deficit is slight, it may reduce cambial activity before affecting the level of photosynthesis in the crown appreciably. In this case, a greater amount of carbohydrates would be available to fewer developing tracheids, resulting in increased secondary thickening (42). It is conceivable that the gradual onset of these conditions at the cambium, coupled with a gradual decrease in terminal elongation, may contribute to the serial earlywood-latewood transition found in eastern white pine.

Keinholz (18) found that cessation of leader growth was more gradual in white pine than in red pine or pitch pine and that the latter two species normally show a more abrupt earlywood-latewood

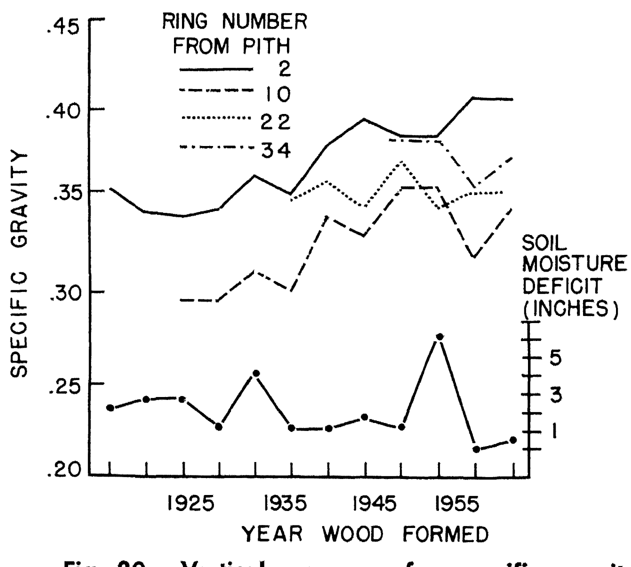


Fig. 20.—Vertical sequences for specific gravity arranged over year of wood formation and current March 1 to October 31 soil moisture deficit.

transition than eastern white pine. Similarly, Buckland (3) found that apical growth ended more sharply in Douglas fir than in grand fir, western hemlock, or western red cedar. The earlywood-latewood transition is more distinct in Douglas fir than in the other three species.

Since, according to Wareing (39), the onset of latewood formation is due in part to a decline in the amount of auxin translocated to the cambium from the more slowly elongating apical zones, the gradualness with which terminal growth ends may be reflected in the transition from earlywood to latewood.

The reasons for the progressive diminution of ring width downwards along a growth sheath are essentially those which apply to the reduction in the number of earlywood cells. This is true for eastern white pine since ring width shows a positive correlation (+.91) with the number of earlywood cells in the growth ring. This indicates that increase in ring width is due to a greater production of tracheids rather than the formation of an equivalent number of larger cells. This is somewhat modified by the fact that moisture deficit is as important as in-stem position in determining ring width.

There appears to be a tendency towards larger tracheid size during low moisture deficits, although this is subordinate to the greater production of tracheids. The configuration of ring width basipetally is a growth sheath found in this study (increasing within the active crown, decreasing rapidly thereafter, and then more slowly towards the base) was similar to that described by Onaka (24) for coniferous trees with crowns of medium size.

Following a given ring from the pith vertically upwards in the stem, ring width diminishes with increasing height in the stem, particularly in rings close to the pith. It is generally true that annual height growth decreases with increasing age. Thus it is possible that, as the length of the leading shoot decreases with age, fewer needles will be produced on the leader of a 40-year-old stem than on the 10-year-old leader of the same tree. Assuming the needles at both ages to be equally efficient, this would result in less photosynthate being available for cellular development in the top of the older stem, giving rise to reduced ring width in the upper levels of a given ring from the pith.

Percentage of Latewood

Number of earlywood cells and ring width both changed in association with soil moisture deficit for the period March 1 to October 31 of the current growing season. Number of latewood cells, however, showed little direct relationship with soil moisture availability, although percentage of latewood fluctuated with soil moisture deficits for the current June 1 to August 31. All four characteristics displayed patterns of behavior apparently dependent in large measure on the number of internodes which the active cambium is removed from the upper crown and current stem apex along a given growth sheath.

An examination of oblique sequences for cell numbers, ring width, and percentage of latewood (Figures 6, 9, and 12) shows clearly that the basipetal increase of the last variable was due to a pronounced decrease in earlywod cells, not to marked increased latewood formation. The amount of latewood varies, but only to the extent of emphasizing the earlywood-determined pattern.

The observations reported here agree only partially with the findings of Smith and Wilsie (32) for loblolly pine in Arkansas. They agree to the extent that percentage of latewood formed varies in association with soil-moisture deficit in the latter part of the year in which the wood is formed. Low soil moisture deficits in Arkansas resulted in a basipetal increase in percentage of latewood, while higher deficits reduced the difference between the top and bottom of the growth sheath. In extreme drought the pattern was reversed, with the highest percentage of latewood formed in the upper part of the growth sheath.

In the white pine examined, conditions were opposite. The percentage of latewood increased with increasing distance from the current stem apex in all instances. Indeed, this pattern was accentuated in years of high soil moisture deficit due to the greater decrease in earlywood, especially in the lower portion of the growth sheath.

Thus, although percentage of latewood is associated with late season soil moisture deficits in both species, a high deficit is associated with high latewood percentage in the top of loblolly pine but with high latewood percentage at the base of eastern white pine.

A correlation coefficient of +.40 was obtained between specific gravity and percentage of latewood, with higher specific gravity associated with higher latewood percentage. With longitudinal shrinkage, the percentage of latewood gave a correlation of —.16, with percentage shrinkage decreasing with increasing percentage of latewood. Both of these relationships were significant at the 1 percent level.

Thus, although the latewood band is narrow and relatively uniform in width in eastern white pine, its proportional variation in regard to total ring width, expressed as percentage of latewood, shows a statistically significant association with longitudinal shrinkage and specific gravity.

As pointed out previously, the measure of latewood in eastern white pine used in this study leaves something to be desired. Therefore, any discussion of this structural property must be regarded as open to error until a more definite characterization can be applied. The data presented here deal with latewood according to Mork's definition but not necessarily with latewood as a physiological function of the annual ring.

Longitudinal Shrinkage

High longitudinal shrinkage in the top internodes of a growth sheath, or close to the pith of the entire tree, is due to a combination of factors (34). First, percentage of latewood is minimal in this part of the stem (Figures 12 and 13). Both Koehler (19) and Cockrell (4) noted that the earlywood component of the growth ring tends to shrink more longitudinally than the latewood portion.

With the low percentage of latewood present, there is a tendency for greater shrinkage close to the apex. As latewood percentage begins to rise steeply at about the 10th internode from the current stem apex, longitudinal shrinkage begins to level off (Figure 21). This is the area where the number of earlywood cells in the growth ring, and hence total ring width, begins to diminish from the maximum values. The coincidence of the major inflection of the four series of curves suggests that, above a certain value, percentage of latewood in the growth ring may exert a restraining influence on the longitudinal shrinkage of the entire ring.

This agrees with Cockrell (5), who showed that latewood in several conifers expanded longitudinally on drying from the green to air-dry state. When an entire ring was oven-dried, the latewood exerted a restraint on the shrinkage of the whole ring.

However, percentage of latewood can not wholly account for the high shrinkage percentage found in the top 6 to 10 internodes of a growth sheath or in the first 10 rings from the pith in a horizontal sequence. This latter zone comprises the so-called "juvenile" wood where tracheids are shorter and have greater fibril angle, lower tensile strength, and higher specific gravity than in growth rings laid down subsequently (8). These properties are similar to those ascribed to compression wood by Pillow and Luxford (27) and Dadswell (7).

While juvenile wood may not be compression wood in the true sense, it has many of the same properties. Of these, fibril angle in the secondary cell wall is possibly the most influential on longitudinal shrinkage. Removal of water from the cell wall results in the fibrils being drawn closer together normal to their long axis. When the fibrils make a small angle with the long axis of the cell, there is little shrinkage in the longitudinal direction. Given a large fibril angle, a greater part of the shrinkage force acts in this plane, with a resultant increase in longitudinal shrinkage. Compression wood, generally, is characterized by a large fibril angle and high longitudinal shrinkage (27).

Development of juvenile, or compression, wood in the top internodes may be caused in part by the high auxin concentrations found in this region. Formation of compression wood in seedlings following high auxin applications was reported by Wershing and Bailey (40). More recently, Wardrop and Davies (38) found compression wood formation to be induced in *Pinus radiata* by the application of 3-indoleacetic acid and gibberellic acid, either separately or together.

In addition to chemical stimulus, compression wood development may be influenced by mechanical stresses imposed on the stem by buffeting winds. Sinnott (30) stimulated compression wood formation by bending stems out of the vertical. It is conceivable that wind force may accomplish the same end.

If the degree of longitudinal shrinkage is associated with the amount of compression wood present, and this in turn is affected by the mechanical bending, it is interesting to note that longitudinal shrinkage of wood formed close to the apex increases with height in the stem. This is illustrated in the vertical sequence for the 2nd ring from the pith in Figure 17. The increase may be due to a progressively greater exposure to sway of the top internodes of the tree with increasing age and height, particularly for dominant and codominant trees such as those used in this study.

The top 6 internodes of a young tree, possibly protected by brush and at the end of a relatively short stem, would be less liable to bending from the vertical than the top 6 internodes of a 50-year-old stem, which are subject to "whiplash" action at the end of a 75-foot cantilever beam. As a corollary, it would be of interest to trace the longitudinal shrinkage pattern in a suppressed stem, progressively more protected from wind sway within the stand. One would expect little or no increase in following upwards the vertical sequence of a ring close to the pith.

A complex of factors apparently affects longitudinal shrinkage along a growth sheath. At lower levels in the mature stem, where the plant is less pliable, longitudinal shrinkage is associated with a limiting value for percentage of latewood. In the upper portion of the sheath, the preponderance of earlywood cells in the ring, high auxin levels, and mechanical bending stresses may be more important. Longitudinal shrinkage appears to be independent of growth rate and of position in the stem beyond 10 rings from the pith.

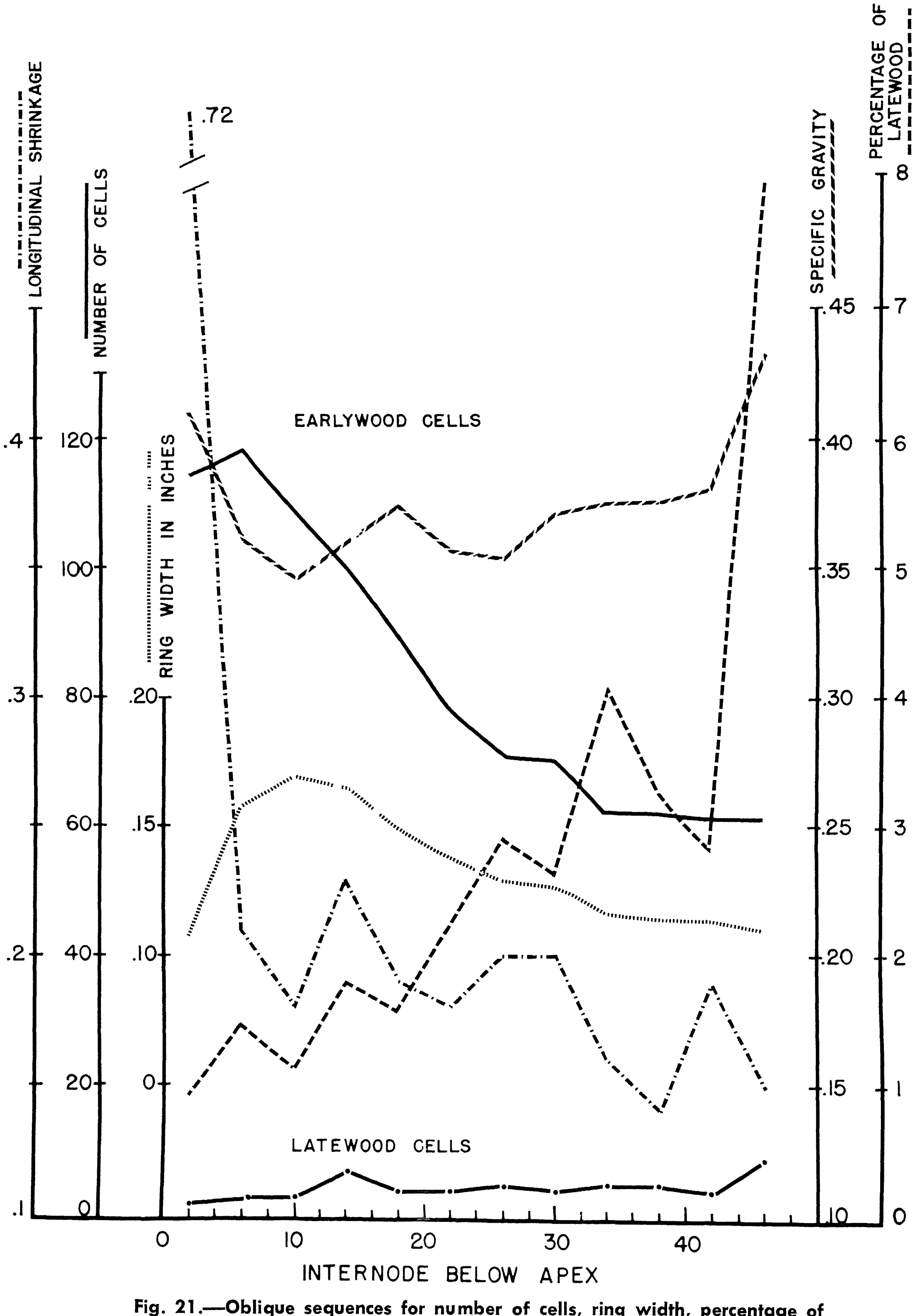


Fig. 21.—Oblique sequences for number of cells, ring width, percentage of latewood, specific gravity, and longitudinal shrinkage in 1961 growing season.

Specific Gravity

Specific gravity is possibly the most studied and most discussed property of wood. This is evident from the numerous references appearing in reviews on the subject (21, 26, 33, 35). Specific gravity is a utilitarian property, lending itself to interpretation in terms of mechanical strength characteristics of wood both as a structural material (2) and as a source of wood fiber (6, 9).

Since it has widely applicable diagnostic qualities, there has been much effort to determine which factors or properties influence specific gravity. Both percentage of latewood and ring width have their protagonists who suggest that these two properties, either separately or together, determine specific gravity.

In the present study, specific gravity showed an inverse relationship with ring width, —.56, and a direct relationship with percentage of latewood, +.40. Both correlations were significant at the 1 percent level. Thus, on following a narrowing growth sheath downward in the stem, the increasing ring volume occupied by cells with marked secondary thickening was associated with increased specific gravity of the entire ring. In species with substantial and varying amounts of latewood in the growth ring, as the southern pines or Douglas fir, one might expect this would affect the specific gravity of the growth ring as described by Larson (21) and Smith (31).

Fegel (12), working with eastern white pine, suggested that width of the earlywood band is the determining variable, with the latewood band having relatively unchanging width. While data from the present study agree with Fegel's observations, these conditions of constant latewood and varying earlywood widths result in changes of latewood percentage associated with changes in specific gravity. Likewise, ring width measurements in the present study were associated with changes in specific gravity. However, it is believed the observations indicate a predominating effect of physiological position relative to the active crown. Thus specific gravity in all growth sheaths decreases to approximately the 10th internode below the current stem apex, then increases gradually to the base of the sheath.

Number of earlywood cells, ring width, and percentage of latewood were all contributing factors, as were others not examined here. However, the dominant influence was cambial distance from the top of the stem. This agrees in substance with Turnbull's (37) thesis that wood density is a function of age rather than of ring width.

While the present study by no means accounted for all of the variables affecting specific gravity of eastern white pine, since $R^2 = 0.429$, the data indicated a repetitive annual pattern in the growth sheaths. When horizontal sequences at given levels in the stem were examined, the curve showed a decrease in specific gravity from the pith to ring 8 or 10, followed by a general increase from this point to the circumference.

The specific gravity at the circumference was frequently as high or higher than that close to the pith. Fluctuations accompanying changes in ring width or percentage of latewood, while consistent in direction, were not large. This finding agreed with Paul's (26) statement that eastern white pine shows little change in specific gravity with change in growth rate.

The view of Fry and Chalk (13), with reference to *Pinus patula*, that distance from the pith and ring width operate together in affecting specific gravity appears applicable to eastern white pine when the distance is measured in terms of annual rings. This pattern has been noted previously (33, 37) and generally ascribed to aging of the cambium. However, aging of the cambium at any level in a tree stem is an expression of increasing physiological distance between the cambium and the upper whorls of the crown and the stem apex. This progressive removal from the active crown primarily determines specific gravity at a given point in a stem, through the effect on the amount of wall substance incorporated into the growth ring.

CONCLUSION

All properties examined showed a definite pattern of variation associated with the number of internodes below the stem apex along a given growth sheath.

For number of earlywood cells and ring width, variation due to position in the stem was large, with a superimposed effect of soil moisture deficit during the period March 1 to October 31 in the current growing season.

Percentage of latewood showed a pattern which, while markedly associated with in-stem position, was strongly related to soil moisture deficit between June 1 and August 31 in the current growing season.

Longitudinal shrinkage and specific gravity appeared virtually independent of soil moisture availability. Although the pattern due to position was well defined, the amount of variation was small.

Thus, the wood of eastern white pine appears to be characterized by relative uniformity of longitudinal shrinkage and specific gravity beyond the 10th ring from the pith, at all heights in the stem, and under varied soil moisture availability conditions.

SUMMARY

The objectives of the study were: (1) to examine variation in cell number in the annual ring, ring width, percentage of latewood, longitudinal shrinkage, and specific gravity existing at different heights in the stem and at different distances from the pith in eastern white pine (*Pinus strobus*); and (2) to examine to what extent change in the above variables is associated with annual and seasonal levels of soil moisture availability.

Three 52-year old eastern white pine were felled in a plantation at Wooster, Ohio. Discs were cut from the middle of each 4th internode, beginning at the 2nd internode from the stem apex and continuing through the 46th internode.

Numbers of earlywood and latewood cells in the growth ring, ring width, and percentage of latewood were recorded for every ring along a north-south diameter on the 12 discs from each tree. Longitudinal shrinkage and specific gravity were recorded for all even-numbered rings from the pith, also along a north-south diameter.

Daily values for maximum and minimum temperatures and precipitation were obtained for the 50 growing seasons prior to felling. These were combined with soils data in an IBM program which estimated daily soil moisture availability over the 50-year period.

Earlywood cells made up the greater part of the growth ring. The number of earlywood cells formed during a growing season fluctuated with soil moisture availability during the period March 1 to October 31, with a greater number of cells being formed in a wet than in a dry year. The number of earlywood cells comprising a growth sheath increased from the 2nd to the 8th internode below the current stem apex, then decreased rapidly to the 20th. At this point the decline became more gradual and on occasion reverted to a slight increase.

The number of latewood cells increased very slightly basipetally along a growth sheath and showed little relationship to soil moisture availability. Ring width varied with earlywood formation, with latewood width relatively constant.

Percentage of latewood increased continuously downwards along a growth sheath with increasing number of internodes below the current stem apex. Latewood percentage varied in association with soil moisture availability during the period June 1 to August 31. Change in percentage of latewood with distance from the apex was due to markedly diminishing numbers of earlywood cells, coupled with a slight increase in the number of latewood cells.

Longitudinal shrinkage showed no relationship with soil moisture availability but there was a definite positional effect within the stem. Shrinkage decreased sharply from the 2nd to the 6th internode in a growth sheath. After the 6th internode, shrinkage fluctuated narrowly, although randomly, about a constant value.

Specific gravity decreased along a growth sheath from the 2nd to the 8th or 10th internode below the current stem apex. Then it increased gradually to the base of the sheath. Association with soil moisture availability was not statistically significant.

The data support the thesis that the pattern of cambial activity along a stem is influenced strongly by the downward flow of carbohydrates and growth regulators, or their precursors, from the upper crown and elongating shoots. All properties examined showed a definite pattern of variation relative to the current stem apex.

For number of earlywood cells and ring width, variation due to position in the stem was large, with an additional effect of current soil moisture deficit. Longitudinal shrinkage and specific gravity appeared virtually independent of soil moisture availability and, although the pattern due to position was precise, the amount of variation was small.

Thus the wood of eastern white pine is characterized by relative uniformity in longitudinal shrinkage and specific gravity beyond the 10th ring from the pith, at all levels in the stem and under varied soil moisture availability conditions.

LITERATURE CITED

1. Bannan, M. W. 1962. Cambial Behavior with Reference to Cell Length and Ring Width in *Pinus strobus* L. Can. Jour. Bot. 40:1057-1062.
2. Brown, H. P., A. J. Panshin, and C. C. Forsaith. 1949. Textbook of Wood Technology, Vol. II. McGraw-Hill Book Co., New York.
3. Buckland, D. C. 1956. Terminal Shoot Growth of Four Western Conifers for a Single Growing Season. For. Chron. 32:397-399.
4. Cockrell, R. A. 1947. Explanation of Longitudinal Shrinkage of Wood Based on an Interconnected Chain-molecule Concept of Cell-wall Structure. Trans., A.S.M.E. 69:931-935.
5. ——————. 1949. Further Observations on Longitudinal Shrinkage of Softwoods. Proc., For. Prod. Res. Soc., 455-459.
6. Curran, C. E. 1936. Some Relations between Growth Conditions, Wood Structure, and Pulping Quality. Paper Trade Jour., Sept. 10, 36-40.
7. Dadswell, H. E. 1957. Tree Growth Characteristics and Their Influence on Wood Structure and Properties. Seventh Brit. Commonwealth For. Conf.
8. ——————. 1960. Tree Growth-Wood Property Interrelationships. Proc., Spec. Field Inst. in For. Biol., Sch. For., Raleigh, N. C.
9. ——————, A. J. Watson, and J. W. P. Nicholls. 1959. What Are the Wood Properties Required by the Paper Industry in Trees of the Future? Tappi 42:521-526.
10. Duff, G. H. and N. J. Nolan. 1953. The Controls of Cambial and Apical Activity in *Pinus resinosa* Ait. Can. Jour Bot. 35:527-572.
11. Echols, R. M. and A. B. Baldwin. 1961. Inexpensive Ring Analyzer for Cumulative Summerwood Measurements. For. Sci. 7:147-148.
12. Fegel, A. C. 1941. Comparative Anatomy and Varying Physical Properties of Trunk, Branch, and Root Wood in Certain Northeastern Trees. N. Y. State Coll. of For., Tech. Pub. 55.
13. Fry, G. and L. Chalk. 1957. Variation of Density in the Wood of*Pinus patula* Grown in Kenya. Forestry 30:29-45.
14. Glock, W. S. 1955. Tree Growth. II. Growth Rings and Climate. Bot. Rev. 21:73-188.
15. Hamilton, J. R. 1961. Variation of Wood Properties in Southern Red Oak. For. Prod. Jour. 11:267-271.
16. Hatcher, E. S. J. 1959. Auxin Relations of the Woody Shoot: the Distribution of Diffusible Auxin in the Shoots of Apple or Plum Rootstock Varieties. Ann. Bot. 23:409-423.
17. Jacobs, M. R. 1945. The Growth Stresses of Woody Plants. C.S.I.R.O., Canberra, Aust., Bull. 28.
18. Keinholz, R. 1934. Leader, Needle, Cambial, and Root Growth of Certain Conifers and Their Interrelations. Bot. Gaz. 96:73-92.
19. Koehler, A. 1931. Longitudinal Shrinkage of Wood. Trans., Amer. Soc. of Eng. 53:17-20.
20. Kramer, P. J. and T. T. Kozlowski. 1960. Physiology of Trees. McGraw-Hill Book Co., New York.
21. Larson, P. R. 1957. Effect of Environment on the Percentage of Summerwood and Specific Gravity of Slash Pine. Yale Univ. School of For., Bull. 63.
22. Larson, P. R. 1963. The Indirect Effect of Drought on Tracheid Diameter in Red Pine. For. Sci. 9:52-62.
23. Mork, E. 1928. The Quality of Spruce Wood with Special Regard to Pulpwood. Papier Fabr. 26:741-747; Abs., Tappi Mono. 24, 1962.
24. Onaka, F. 1950. The Longitudinal Distribution of Radial Increment in Trees. Kyoto Univ., For. Bull. 18.
25. Ordin, L. 1960. Effect of Water Stress on Cell Wall Metabolism of *Avena* Coleoptile Tissue. Plant Phys. 35:443-450.
26. Paul, B. H. 1963. The Application of Silviculture in Controlling the Specific Gravity of Wood. U. S. Dept. Agr., Tech. Bull. 1288.
27. Pillow, M. Y. and R. F. Luxford. 1937. Structure, Occurrence, and Properties of Compression Wood. U. S. Dept. Agr., Tech. Bull. 546.
28. Richardson, S. D. 1961. A Biological Basis for Sampling in Studies of Wood Properties. Tappi 44:170-173.
29. Roberts, B. R. 1964. Effect of Water Stress on the Translocation of Photosynthetically Assimilated Carbon-14 in Yellow Poplar. *In* The Formation of Wood in Forest Trees. Academic Press, Inc., New York, pp. 273-288.
30. Sinnott, E. W. 1952. Reaction Wood and the Regulation of Tree Form. Amer. Jour. Bot. 37:69-78.
31. Smith, D. M. 1955. Relationship between Specific Gravity and Percentage of Summerwood in Wide-ringed, Second-growth Douglas Fir. U. S. Dept. Agr., For. Prod. Lab. Rep. 2045.

32. ———— and M. C. Wilsie. 1961 Some Anatomical Responses of Loblolly Pine to Soil-water Deficiencies. Tappi 44:179-185.
33. Spurr, S. H. and W. Hsiung. 1954. Growth Rate and Specific Gravity in Conifers. Jour. For. 52.191-200.
34. ———— and M. J. Hyvarinen. 1954. Compression Wood in Conifers as a Morphogenetic Phenomenon. Bot. Rev 20:551-560
35. Tappi Monograph 24. 1962. The Influence of Environment and Genetics on Pulpwood Quality. Tech Assoc. of the Pulp and Paper Ind., New York.
36. Thornthwaite, C. W. 1948. An Approach toward a Rational Classification of Climate Geograph. Rev. 38:55-94.
37. Turnbull, J. M. 1947. Some Factors Affecting Wood Density in Pine Stems. Union of South Africa For. Dept., Pub 84.
38. Wardrop, A. B. and G. W. Davies. 1964 The Nature of Reaction Wood. VII. The Structure and Differentiation of Compression Wood. Aust. Jour. Bot. 12:24-38.
39. Wareing, P. F., C. E. A. Hanney, and J. Digby. 1964 The Role of Endogenous Hormones in Cambial Activity and Xylem Differentiation. *In* The Formation of Wood in Forest Trees. Academic Press, Inc., New York.
40. Wershing, H. F. and I. W. Bailey. 1942. Seedlings as Experimental Material for the Study of "Redwood" in Conifers. Jour. For. 40:411-414.
41 Westerveldt, F. H. 1962. Regression Analysis Program on the 709/7090. Unpublished Paper, Computing Center, Univ. of Mich., Ann Arbor.
42. Zahner, R. 1963. Internal Moisture Stress and Wood Formation in Conifers. For. Prod. Jour. 13:240-247.
43. ———— and A. R. Stage. 1963. Instructions for Using the University of Michigan Program for Computing the Daily Water Balance, Water Deficits by Periods, and Coefficients for a Regression of Yield on Weather. Unpublished Paper, Sch. of Nat. Resources, Univ. of Mich., Ann Arbor.